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https://doi.org/10.11646/zootaxa.4579.1.1 http://zoobank.org/urn:lsid:zoobank.org:pub:A4015309-D9B3-4BB7-ABCB-B88A1F8CE5FC

# ZOOTAXA



# Mesoparasitic copepods (Copepoda: Cyclopoida) associated with polychaete worms in European seas

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Magnolia Press Auckland, New Zealand

Accepted by E. Suárez-Morales: 25 Feb. 2019; published: 9 Apr. 2019

GEOFF A. BOXSHALL, MYLES O'REILLY, ANDREY SIKORSKI & REBECCA SUMMERFIELD **Mesoparasitic copepods (Copepoda: Cyclopoida) associated with polychaete worms in European seas** (*Zootaxa* 4579)

69 pp.; 30 cm.

9 Apr. 2019

ISBN 978-1-77670-628-0 (paperback)

ISBN 978-1-77670-629-7 (Online edition)

FIRST PUBLISHED IN 2019 BY Magnolia Press P.O. Box 41-383 Auckland 1346 New Zealand e-mail: magnolia@mapress.com https://www.mapress.com/j/zt

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ISSN 1175-5326(Print edition)ISSN 1175-5334(Online edition)

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# Abstract

A large collection of mesoparasitic copepods from polychaete hosts collected in northern European waters was examined. The term mesoparasitic refers to highly transformed copepods where the adult female attaches by embedding part of its body in the host. Representatives of five known familes were found and a new family is established. A single new species, Bradophila minuta sp. nov., was described in the family Bradophilidae. It occurred exclusively on the flabelligerid Diplocirus glaucus (Malmgren, 1867). Two genera of the family Herpyllobiidae were represented: Herpyllobius Steenstrup & Lütken, 1861 and Eurysilenium M. Sars, 1870. Herpyllobius arcticus Steenstrup & Lütken, 1861 was found on at least five different polynoid hosts, two of which, Harmothoe fragilis Moore, 1910 and Antinoe sp., were new host records. A new species, H. cluthensis sp. nov. was described from Malmgrenia species in Scottish waters. The large species, Herpyllobius cordiformis Lützen, 1964, was collected in Arctic waters from Eunoe cf. oerstedi. It is the first report of this parasite in Europe. The common parasite H. polynoes (Krøyer, 1864) was found on six different polynoid hosts, three of which, Harmothoe bifera, Malmgreniella mcintoshi Tebble & Chambers, 1982 and Eunoe ?barbata are new host records. Eurysilenium truncatum M. Sars, 1870 was collected from Eucranta villosa Malmgren, 1866, Eunone sp., and Gattyana cirrhosa (Pallas, 1766). The material from Eucranta villosa caught at 72.6°N comprises both a new host record and is the most northerly report of this parasite. Specimens of Eurysilenium which differed from E. truncatum in a number of features were found on Harmothoe fragilis and H. impar (Johnston, 1839). A new family, the Pholoicolidae, is established to accommodate Pholicola chambersae gen. et sp. nov., parasitic on Pholoe pallida Chambers, 1985. The family Phyllodicolidae was represented by all three of its known species: Phyllodicola petiti (Delamare Deboutteville & Laubier, 1960), Cyclorhiza eteonicola Heegaard, 1942 and C. megalova Gotto & Leahy, 1988. The former was found on Eumida ockelmanni Eibye-Jacobsen, 1987, a new host record. A single ovigerous female of C. eteonicola was collected from a new host, Eteone spetsbergensis Malmgren, 1865. Cyclorhiza megalova was common on Eteone longa (Fabricius, 1780) and E. longa/flava complex. A rich diversity of members of the family Saccopsidae was found, including three known species of Melinnacheres M. Sars, 1870 plus nine new species placed in four new genera. Melinnacheres was represented by M. ergasiloides M. Sars, 1870, M. steenstrupi Bresciani & Lützen, 1961 and M. terebellidis Levinsen, 1878. Melinnacheres ergasiloides was found on Melinna elizabethae McIntosh, 1914, M. steenstrupi on members of the Terebellides stroemi-complex and T. atlantis Williams, 1984, while M. terebellidis was found on the T. stroemi-complex and on T. shetlandica Parapar, Moreira & O'Reilly, 2016. A new genus, Trichobranchicola gen. nov., was established to accommodate T. antennatus gen. et sp. nov., a parasite of Trichobranchus sikorskii Leontovich & Jirkov in Jirkov, 2001, T. glacialis Malmgren, 1866 and Trichobranchus sp. The second new genus, Lanassicola gen. nov., was established to accommodate the type species, Lanassicola arcticus gen. et sp. nov. parasitic on Lanassa venusta (Malm, 1874), plus two additional species, L. bilobatus gen. et sp. nov. on Lanassa nordenskjoeldi Malmgren, 1866, and L. dorsilobatus gen. et sp. nov. on Proclea graffii (Langerhans, 1884). A new subfamily, Euchonicolinae, was established within the Saccopsidae to accommodate two new genera, Euchonicola gen. nov. and Euchonicoloides gen. nov. The type species of Euchonicola gen. nov. is E. caudatus gen. et sp. nov., a parasite of Euchone sp., and it includes two other species, E. linearis gen. et sp. nov. on Chone sp., and E. parvus gen. et sp. nov. on Euchone sp. The type species of Euchonicoloides gen. nov. is E. elongatus gen. et sp. nov. found on a host belonging to the genus Euchone, and it also includes Euchonicoloides halli gen. et sp. nov. from Jasmineira caudata Langerhans, 1880. Four species of the family Xenocoelomidae were found: Xenocoeloma alleni (Brumpt, 1897), X. brumpti Caullery & Mesnil, 1915, X. orbicularis sp. nov. and Aphanodomus terebellae (Levinsen, 1878). Xenocoeloma alleni was found on four different species of Polycirrus and on Amaeana trilobata (M. Sars, 1863) and X. brumpti was found on Polycirrus norvegicus Wollebaek, 1912. Xenocoeloma orbicularis sp. nov. occurred only on Paramphitrite birulai (Ssolowiew, 1899). Aphanodomus terebellae was found on three hosts, only one of which, Leaena abranchiata was new.

Key words: parasitic copepod, polychaete host, new genera, new species, taxonomy

# Introduction

There has been a long history of studies on parasitic copepods from polychaete hosts in northern European waters. Indeed, many of the highly transformed copepod genera found in association with polychaetes were originally described in the late Nineteenth Century from material taken in North Atlantic waters and investigated by Scandinavian researchers, including species of *Herpyllobius* Steenstrup & Lütken, 1861, *Eurysilenium* M. Sars, 1870, *Bradophila* Levinsen, 1878, and *Melinnacheres* M. Sars, 1870 (Steenstrup & Lütken 1861; Krøyer 1864; M. Sars 1870; Levinsen 1878). The emphasis of the pioneering work of these authors was typically on external morphology and elucidation of life cycles, but much of the subsequent detailed anatomical work has also been performed by Scandinavian researchers, in particular, by Bresciani and Lützen (Bresciani & Lützen 1961, 1966, 1974, 1975; Lützen 1964a,b, 1966, 1968).

This paper is based on parasitic copepods collected from polychaete hosts that have been examined during the processing of large samples of macrobenthic invertebrates mostly from Norwegian and British and Irish waters. It is the third in a planned series of papers based on such material: in the first, Kim *et al.* (2013) reported on 12 new species belonging to the nereicoliform group of families and provided re-descriptions of another six. In the second, a new family of mesoparasitic copepods was established, the Jasmineiricolidae Boxshall, O'Reilly, Sikorski & Summerfield, 2015, based on material parasitic on species of the sabellid polychaete *Jasmineira* Langerhans, 1880 (Boxshall *et al.* 2015). The focus of this third account is on other families of mesoparasitic copepods: parasites that typically have adult females with highly transformed bodies and that live with part of the body, the endosoma, embedded within the host and part, the ectosoma, lying external to the host.

# Material and methods

Copepod specimens attached to or embedded in their polychaete hosts were examined as whole preparations either after immersion in lactic acid for periods between 1 h and 48 h, or whilst in preservative (80% ethanol). After microscopic observation on the host, the copepods were removed from the host by dissection. Intact and dissected specimens were examined as temporary preparations in lactic acid on a Leitz Diaplan microscope equipped with differential interference contrast optics. All drawings were made using a drawing tube. Material for scanning electron microscopy (SEM) was washed three times in distilled water, dehydrated through graded acetone series, critical point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with palladium. Coated material was examined using a Phillips XL30 Field Emission Scanning Electron microscope operating at 5 Kv. Two images (Figures 4 and 12) were captured by Micro-CT (Nikon HMXST 225, Nikon Metrology, Tring UK). The methods of specimen preparation, examination and image processing are as described in Boxshall *et al.* (2015).

Morphological terminology follows Huys & Boxshall (1991) and host nomenclature was checked against the World Register of Marine Species (WoRMS Editorial Board 2018). We use the term polychaete in the traditional vernacular sense to encompass those predominantly marine, segmented annelid worms with parapodia and nuchal organs (e.g. as defined in Ruppert *et al.* 2004). Type and voucher specimens are deposited in the collections of the Natural History Museum, London.

# **Systematics**

# Order Cyclopoida Burmeister, 1834

# Family Bradophilidae Marchenkov, 2002

The genus *Bradophila* Levinsen, 1878 was originally described by Levinsen (1878) but over 120 years later, it was Marchenkov (1999) who first suggested that it belonged in a separate family and later he formally established the family (Marchenkov 2002). The genus and family have remained monotypic until recently, although Boxshall & Halsey (2004) suggested a possible relationship with the poorly known *Trophonophila bradii* M'Intosh, 1885, which also occurs on a flabelligerid polychaete host, taken in deep water to the south of Australia (M'Intosh 1885). Huys (2016) re-examined the holotype female of *T. bradii* and confirmed that this genus is a member of the Bradophilidae. Huys (2016) also considered that the name of the species should be changed to *T. bradyi* as M'Intosh (1885) explicitly named the species after George Stewardson Brady. However, since the original spelling given by M'Intosh (*bradii*) clearly constitutes an attempt at the latinization of Brady's name, we retain the original spelling in accord with ICZN Art. 32.5.1, which states that incorrect latinization is not to be considered an inadvertent error.

The globular and limbless ectosoma of adult female *Bradophila* resembles that of females of the family Herpyllobiidae, but these two families differ markedly in the structure of the males: *Bradophila* males have well-developed, prehensile antennae which are used to attach to the ectosoma of the female, plus recognizable antennules, mandibles, maxillules, maxillae, and maxillipeds (Marchenkov 2002; Huys 2016). In contrast, male

herpyllobiids lack all cephalothoracic appendages except for males of *Gottoniella* López-González, Bresciani & Conradi, 2006, which possess a pair of 3-segmented subchelate limbs, identified as probably the maxillipeds by López-González *et al.* (2006), and males of *Eurysilenium* which possess a pair of stylet-like structures of uncertain affinity in the oral region (Lützen 1964a).

# Genus Bradophila Levinsen, 1878

**Diagnosis**. Adult female body highly transformed consisting of ectosoma connected to endosoma by broad stalk passing through host's body wall. Endosoma embedded in host, elongate, filiform. Ectosoma globular to slightly dorsoventrally flattened; lacking any external trace of segmentation. Genital apertures paired, carried on sclerotized areas of cuticle located posterolaterally on margin of ectosoma; median copulatory pore located between genital apertures on ventral surface of ectosoma. Lacking vestiges of appendages and caudal rami; without anus. Egg sacs paired, large, multiseriate.

Adult male consisting of broad, subquadrate cephalothorax and slender postcephalic trunk. Caudal rami modified as pair of hooks. Antennule indistinctly 3-segmented; third segment offset posterolaterally; first segment with blunt, modified setal element; second segment with 2 setal elements; distal segment with 2 apical elements. Antenna uniramous and subchelate, comprising elongate proximal segment, plus distal endopodal segment bearing terminal claw plus accessory claw. Mandible absent. Maxillule small, lobate, bearing 2 apical setae. Maxilla lobate, ornamented with denticles distally. Maxilliped subchelate; proximal segment robust, ornamented with 2 spinulose processes on myxal surface; distal subchela comprising free endopodal segment plus curved claw.

Type species: Bradophila pygmaea Levinsen, 1878, by monotypy.

**Remarks.** Since its original description 140 years ago, the type species, *B. pygmaea*, has been reported from only a single host species, *Brada villosa* (Rathke, 1843), a member of the polychaete family Flabelligeridae de Saint Joseph, 1894. The original description was based on museum material with no locality data (Levinsen 1878) but its known distribution is restricted to high latitude waters of the North Atlantic including both Norwegian and Russian coastal waters and into the White Sea (Marchenkov 1999; Huys 2016). Marchenkov (2002) gave supplementary morphological data on the female of *B. pygmaea*: its globular, slightly flattened ectosoma ranged from 0.5 to 0.7 mm in diameter; the egg sacs were up to 1.2 mm long and varied in width from 0.4 to 0.7 mm; in live specimens the colour of the ectosoma was translucent or milky white. Marchenkov (2002) stressed that the posterolaterally-located, paired genital apertures of the female were relatively inconspicuous. He also described the endosoma as elongate with its entire surface covered with small tubercles and this was confirmed by Huys (2016). However, as noted by Huys (2016), the size of the ectosoma of the female given by Levinsen (1878) was 330–500 µm, which is considerably smaller than that reported by Marchenkov (2002).

The male of *B. pygmaea* was attached in the vicinity of the stalk of the female by means of its modified caudal rami, antennae and maxillipeds (Marchenkov 2002). Marchenkov gave the male body length as 0.35 to 0.45 mm, with a maximum width at the cephalosome of 0.15 to 0.20 mm. Huys (2016) examined material of *B. pygmaea* and described the male as 530  $\mu$ m in length with a maximum width of 93  $\mu$ m. The structure and setation of the male limbs were described by Marchenkov (2002), and again more recently by Huys (2016) who corrected several misinterpretations made by Marchenkov (2002).

# Bradophila minuta sp. nov.

**Type material**: Holotype ovigerous  $\bigcirc$  from *Diplocirrus glaucus* (Malmgren, 1867), Finnmark, Stn 657-1 (70.8933°N, 25.54°E), depth 93 m, 18 September 2003; collected by A. Sikorski; NHMUK Reg. No. 2015.2991. 1 ovigerous paratype  $\bigcirc$  from *D. glaucus*, 4315 Valhall Norflanken, Stn 14-3 (56.323°N, 03.349012°E), depth 66 m, 30 May 2008; collected by A. Sikorski; NHMUK Reg. No. 2015.2992. 1 ovigerous paratype  $\bigcirc$  from *D. glaucus*, 05.9406°E), depth 154 m, 25 May 2004; collected by A. Sikorski; NHMUK Reg. No. 2015.2993. 1 paratype  $\bigcirc$  from *D. glaucus*, FFH 3958, Stn B1-B (65.9101°N, 12.22313°E), depth 72 m, 23 March 2007; collected by A. Sikorski; NHMUK Reg. No. 2015.2994. 1 ovigerous paratype  $\bigcirc$  from *D. glaucus*, 7165 Sjøtroll C, Stn Ra 3-2 (60.58243°N, 05.177083°E), depth 203 m, 04 September 2014; collected by A.

Sikorski; NHMUK Reg. No. 2016.513. 3 ovigerous paratype  $\bigcirc \bigcirc$  from 3 specimens of *D. glaucus*, 8854 Søprvika, Stn C3 (68° 28.262'N 15° 13.159'E), depth 150 m, 26 April 2017; collected by A. Sikorski, NHMUK Reg. No. 2017.167-169.

Additional non-type material:  $1^{\circ}$  from unidentified polychaete fragment, Oseberg Øst, Stn 9-2 (60.69733°N, 02.929333°E), depth 153 m, 17 May 1997; collected by A. Sikorski. 1 ovigerous  $^{\circ}$  in oral cavity of *D. glaucus*, Western Isles, Loch Seaforth, Maaruig, SEPA Stn Ref. 8 (57° 57.532'N, 06° 43.343'W), depth 19 m, 23 August 2001. 1 ovigerous  $^{\circ}$  in oral cavity of *D. glaucus*, Northumberland, CEFAS End 6/04, Stn 91 (55° 3.690'N, 01° 21.883'W), depth 32 m, 03 June 2004. 1 $^{\circ}$  ovigerous, protruding from prostomial region of *D. glaucus*, Northumberland, Blyth, ENTEC, 2010, collected by P. R. Garwood. 1 ovigerous  $^{\circ}$  in oral cavity of *D. glaucus*, BEN14-0186 (APEM 55898), Irish Sea (53° 48.947'N, 05° 05.814'W), 24 November 2014. 1 ovigerous  $^{\circ}$  in oral cavity of *D. glaucus*, Sund of Jura, 10 km East of the Small Isles, SEPA Stn SJ1 (55° 50.507'N, 05°46.829'W) depth 174 m, 18 May 2016. NHMUK Reg. No. 2018.110-111.

**Differential diagnosis**. Adult female body highly transformed, lacking any external trace of segmentation, consisting of dorsoventrally flattened ectosoma connected to endosoma by broad stalk passing through host's body wall (Fig. 1A). Ectosoma about 1.28 times wider than long (range 1.16 to 1.39 times); mean width 248  $\mu$ m, range 230 to 264  $\mu$ m (based on 3 specimens); mean length 192  $\mu$ m, range 180 to 209  $\mu$ m. Dorsal surface flat, marked with faint longitudinal cuticular ridges in all specimens (Fig. 1B, C); ventral surface smooth (Fig. 1D) but protruding posteroventrally to form wedge-shaped transverse expansion (Fig. 1C). Genital apertures paired, carried on highly sclerotized genital swellings at posterolateral angles of ectosoma (Fig. 1E). Median copulatory pore located on midline between genital apertures (arrowed in Fig. 1E): copulatory duct extending anteriorly, opening into paired seminal receptacles. No vestiges of paired appendages present; caudal rami absent; anus lacking. Egg sacs paired, up to 1.49 mm long and 0.38 mm wide; multiseriate, with maximum of only 3 or 4 longitudinal series of ectosoma. Endosoma slender, flattened, and about 2 mm long with more-or-less parallel margins (Fig. 1A).

Male unknown.

Etymology. The name of the new species, *minuta*, alludes to its small body size.

**Remarks**. The ectosoma of the new species has a slightly different shape from the type species *B. pygmaea*. The ectosoma is dorsoventrally flattened with a wedge-shaped posteroventral protrusion, while in *B. pygmaea* it was described as globular and slightly flattened by Marchenkov (2002). The globular ectosoma of *B. pygmaea* has a diameter in the range of about 0.33 to 0.7 mm according to Levinsen (1878) and Marchenkov (2002), whereas the ectosoma of *B. minuta* **sp. nov**. is distinctly wider than long, and its maximum width of 0.23 to 0.26 mm falls outside the range reported for *B. pygmaea*. The paired genital apertures of *B. pygmaea* were described as relatively inconspicuous by Marchenkov (2002), whereas those of *B. minuta* **sp. nov**. are prominent (Fig. 1E). Another obvious difference between the new species and *B. pygmaea* is the form of the egg sacs: in *B. pygmaea* the egg sacs are very broad in the middle and taper strongly towards each end, and they contain numerous eggs in a multiseriate arrangement with about 7 or 8 complete rows visible in the middle section of each sac, from any view (Levinsen 1878). In contrast, in the new species the egg sacs are cylindrical, maintaining a more or less constant diameter along most of their length, and only 3 to 4 rows of eggs are visible from any view (Fig. 1B). The differences in size and shape of the ectosoma, in the prominence of the genital apertures, and in the arrangement of eggs within the egg sacs support the establishment of a new species, *B. minuta*.

The form of the endosoma of adult female *B. pygmaea* was poorly documented by Levinsen (1878). Marchenkov (2002) described his females as having an elongate endosoma with a tuberculate surface, although he stated that the endosoma was variable in form. The endosoma of the new species is elongate, flattened and lies in the host's coelom around the outside of the gut, as described by Marchenkov (2002). We found the endosoma difficult to observe and not easy to delimit from the surrounding host tissues.

The only known host of *B. pygmaea* is the flabelligerid *Brada villosa*. The new species utilizes a different flabelligerid, *Diplocirrus glaucus*, as host, and the adult female copepods are usually embedded in the tip of the proboscis of the host. The female copepod is normally mostly concealed within the oral cavity of the host with only the tip of the ectosoma or the ovisacs protruding out of the oral aperture. The known depth range of the new species is 19 to 203 m.



**FIGURE 1**. *Bradophila minuta* **sp. nov**. A, habitus of embedded adult female, dorsal view showing elongate flattened endosoma; B, ectosoma and basal part of endosoma of ovigerous female, ventral; C, ectosoma and base of endosoma of female, posterior; D, ectosoma of female, dorsal; E, ectosoma of female, ventral view showing outline of seminal receptacles, and median copulatory pore (arrowed). Scale bars: A, 0.5 mm, B–D, 200 μm, E, 100 μm.

# Family Herpyllobiidae Hansen, 1892

Three genera of Herpyllobiidae, *Herpyllobius, Eurysilenium* and *Phallusiella* Leigh-Sharpe, 1926, were listed as accepted by Boxshall & Halsey (2004) and a fourth, *Gottoniella* López-González, Bresciani & Conradi, 2006, was added later (López-González et al. 2006). The genera *Herpyllobius, Eurysilenium*, and *Gottoniella* are valid but there remains considerable uncertainty over the validity of *Phallusiella*. It was provisionally maintained by Lützen (1964a) but the descriptions of the known species are inadequate by modern standards and possibly inaccurate as well. *Phallusiella* comprises two species, *P. psalliota* Leigh-Sharpe, 1926 and *P. vera* Leigh-Sharpe, 1926, both described from UK waters off Plymouth (Leigh-Sharpe 1926). The host of *P. psalliota* was given as *Harmothoe extenuata* (Grube, 1840) by Leigh-Sharpe (1926), a known host of *Herpyllobius arcticus* Steenstrup & Lütken, 1861. The host of *P. vera* was given as *Malmgrenia castanea* (McIntosh, 1876). The type material could not be traced and, given the lack of any subsequent reports of either of these two species, we consider *Phallusiella* to be a *genus inquirendum* and both *P. psalliota* and *P. vera* to be *species inquirenda*.

The genus *Thylacoides* Gravier, 1912 was not considered by Lützen (1964a) in his review of the family and was overlooked by Boxshall & Halsey (2004). Gravier (1913) considered his genus to be closely related to *Eurysilenium* and proposed *Eurysileniopsis* as a replacement name for *Thylacoides*, because of the latter's close similarity to *Thylacodes* which he regarded as already having been used by Guettard in 1774 stating "ce nom a déjà étè employé par Guettard en 1774". However, *Eurysileniopsis* Gravier, 1913 is an unnecessary replacement name because *Thylacoides*, as established by Gravier (1912 a, b), is not a strict homonym of *Thylacodes*. Gravier's (1913) detailed description of *Thylacoides sarsi* Gravier, 1912 (under the name *Eurysileniopsis sarsi*) is difficult to interpret. It resembles a herpyllobiid in general form, i.e., in possessing a sac-like body attached to host by stalk ("acetabulum") which originated in the middle of the underside of the body, but Gravier (1913) described a "buccal complex" located between the origins of the paired egg sacs. We infer, from its size and position on the body, that the "buccal complex" of Gravier probably represents the paired genital apertures, possibly with males attached. The host of *T. sarsi* was a syllid polychaete, *Trypanosyllis gigantea* (McIntosh, 1885), and only polynoid and aphroditid worms are currently known to serve as hosts for members of the Herpyllobiidae. In the absence of new material we treat *Thylacoides sarsi* as a *species inquirendum*, and its affinities with the Herpyllobiidae are in need of confirmation.

# Genus Herpyllobius Steenstrup & Lütken, 1861

**Diagnosis**. Adult female ectosoma spherical to ovoid or dorsoventrally flattened, bilaterally symmetrical, with prominent and heavily sclerotized paired genital openings posteriorly. Stalk originating on ventral surface in midline, anterior to genital openings. Endosoma varying in shape from irregular 3-dimensional mass, with or without rounded or digitiform lobes, to elongate or discoid flattened process. No vestiges of limbs retained in adult female. Egg sacs paired, multiseriate. Adult male attached to ectosoma of female by means of frontal process; body unsegmented, limbless, bottle-shaped containing paired spermatophores.

Late male copepodid cyclopiform, comprising 4-segmented prosome and 3-segmented urosome. Antennule 3segmented. Maxilliped subchelate. Legs 1 and 2 biramous, with 2-segmented exopods and 1-segmented endopods. Leg 3 biramous, with 1-segmented rami. Leg 4 represented by single seta. Nauplius lecithotrophic, lacking naupliar eye.

Type species: *Herpyllobius arcticus* Steenstrup & Lütken, 1861, by monotypy.

**Remarks**. Males of *Herpyllobius* attach in the vicinity of the genital apertures of the female and often remain within the exuvium of the preceding final copepodid stage. They have an unsegmented, limbless and bottle-shaped body which is attached to the ectosoma of the female by the slender anterior region (the "neck" of the bottle), secured by means of a secretion produced by a frontal gland (Lützen 1966). Males typically attach in the vicinity of the sclerotized dots in the female genital region in species such as *H. polynoes* (Krøyer, 1864) and *H. arcticus*, or near the sclerotized swelling located between the genital apertures in species such as *H. cordiformis* Lützen, 1964 (Lützen 1966). Lützen (1966) stated that *Herpyllobius* males "emit two very long and slender tubes from their frontal part; these are extensions from a pair of sacs". Levinsen (1878) and Hansen (1892, 1900) considered these sacs to be the testes whereas Jensen (1900) interpreted them as spermatophores. Lützen (1964a, 1966) interpreted

them as most likely spermatophores and observed that their tubules "enter the female genital openings" and "introduce the contents of the spermatophores into the receptaculum seminalis" of the female. We support Lützen's interpretation and we note that the spermatophores in *Herpyllobius* are discharged anteriorly through the frontal process of the bottle-shaped adult male. Males of *Herpyllobius* do not have posteriorly-located paired genital apertures.

There are currently 17 valid species of Herpyllobius (Walter & Boxshall 2018): H. antarcticus Vanhöffen, 1913 from Polyeunoa laevis McIntosh, 1885 (as Enipo rhombigera) and Harmothoe fullo (Grube, 1878) (as H. gourdoni Gravier); H. antepositus Stock, 1986 from Lagisca irritans Marenzeller, 1904; H. arcticus from Austrolaenilla mollis (Sars, 1872), Gattyana cirrhosa (Pallas, 1766), Harmothoe extenuata, H. imbricata Linnaeus, 1767, and H. impar (Johnston, 1839); H. australis Lützen, 1964 from Harmothoe spinosa Kinberg, 1856; H. cordiformis from Eunoe nodosa (Sars, 1861); H. elongata Lützen, 1967 from Grubeopolynoe tuta (Grube, 1855) (as Holopidella tuta); H. gravieri Lützen, 1964 from Harmothoe spinosa; H. haddoni Lützen, 1964 from Harmothoe imbricata; H. hartmanae Lützen & Jones, 1976 from Laetmonice producta Grube, 1876; H. lobosaccus Stock, 1986 from Lagisca irritans Marenzeller, 1904; H. luetzeni López-González & Bresciani, 2001 from Harmothoe cf. spinosa; H. nipponicus Lützen, 1964 from Parahalosydna pleiolepis (Marenzeller, 1879); H. polasterni López-González, Bresciani & Conradi, 2000 from Eulagisca gigantea Monro, 1939; H. polynoes from Austrolaenilla mollis, Bylgides promamme (Malmgren, 1867) (as Antinoe badia), B. sarsi (Kinberg in Malmgren, 1866) (as Antinoe sarsi), Eunoe nodosa, Gattyana amondseni (Malmgren, 1867), G. cirrhosa, Gaudichaudius iphionelloides (Johnson, 1901) (as Gattyana iphionelloides), Harmothoe antilopes McIntosh, 1876, H. aspera (Hansen, 1878), H. extenuata, H. imbricata, and H. impar; H. rotundus Lützen & Jones, 1976 from Harmothoe sp.; H. stocki López-González, Bresciani & Conradi, 2000 from Austrolaenilla antarctica Bergström, 1916; and H. vanhoeffeni López-González & Bresciani, 2001 from Eulagisca corrientis McIntosh, 1885. The great majority of these species are reported from high latitude waters (Vanhöffen 1913; Lützen 1964a; López-González & Bresciani 2001; López-González et al. 2000, 2006) and all are recorded from polynoid hosts with the exception of H. hartmanae which utilises a polychaete host from the family Aphroditidae (Lützen & Jones 1976).

# Herpyllobius arcticus Steenstrup & Lütken, 1861

# Syn: Sarsilenium crassirostris Leigh-Sharpe, 1926

**Norwegian material examined**:  $1 \Leftrightarrow$  with  $\checkmark$  attached, from *Harmothoe fragilis* Moore, 1910, Huldra, Stn 1-5 (60.85328°N, 02.65085°E), depth 121 m, 23 May 2004; collected by A. Sikorski; NHMUK Reg. No. 2015.2954.  $2 \Leftrightarrow \bigcirc$  on 2 specimens of *H. fragilis*, Kakshauger, Stn 16-2,4 (59.7336°N, 02.556497°E) depth  $\approx$ 100m, 12 June 2000; collected by A. Sikorski; NHMUK Reg. No. 2015.2955-2956. 1 immature  $\diamondsuit$  from *H. fragilis*, Statfjord C, Stn 6-3 (61.23832°N, 02.043427°E), depth 140 m, 15 June 2005; collected by A. Sikorski; NHMUK Reg. No. 2015.2957. 1 immature  $\diamondsuit$  with 3  $\checkmark \circlearrowright$  attached, from *H. fragilis*, Gullfaks Satelitter, Stn F/G2-4 (61.0931°N, 02.27979°E), depth 133 m, 02 June 2005; collected by A. Sikorski; NHMUK Reg. No. 2015.2958. 1  $\Leftrightarrow$  from *Antinoe* sp., Snorre, Stn Ref 10-8 (61.5115°N, 02.007002°E), depth 311 m, 03 June 1999; collected by A. Sikorski; NHMUK Reg. No. 2015.2959. 1  $\Leftrightarrow$  from *Harmothoe antilopes* McIntosh, 1876, Statfjord N, Stn Ref 8-3 (61.4815°N, 01.852°E), depth 266 m, 08 June 1999; collected by A. Sikorski; NHMUK Reg. No. 2015.2960.

05° 28.395W), depth 87.4 m, 08 September 2006. 1♀ from *Harmothoe* sp., Unico 42471, Survey EHS-SSDM07, Belfast Lough / North Channel, Stn DGM-a (54° 45.00'N, 05° 29.59'W), depth 86 m, 11 April 2007. 1 ovigerous ♀, from *Harmothoe* sp., Unico. 44856, EHS-FEPA08, Stn SDCS-a, (54° 50.51'N, 05° 42.85'W), depth 17 m, 08 April 2008. 1 ovigerous ♀ from *Harmothoe ?impar*; Unico 46998, Survey EHS-FEPA09, Belfast Lough/North Channel, Stn DEM-b, (54° 45.00'N, 05° 29.59'W), depth 86 m, 24 February 2009. 1♀ from *Harmothoe* sp., Unico 47568, Mourne Coast, EHS Stn ANA-C (54° 44.12'N, 05° 55.04'W), depth 19 m, 05 May 2010. NHMUK Reg. Nos 2018.112-121.

**Differential diagnosis** based on females from *Harmothoe fragilis*. Adult female ectosoma almost spherical; mean diameter 1.08 mm, ranging from 0.95 to 1.20 mm in ovigerous females. Genital swellings small, subrectangular (220 to 240  $\mu$ m in height, by 165 to 170  $\mu$ m wide) separated by gap of about 75  $\mu$ m. Four minute sclerotized dots arranged in arc on postero-dorsal surface, above genital swellings. Egg sacs short and thick (1.00 mm in length by 0.56 mm in diameter), typically as long as or just longer than mean diameter of ectosoma. Stalk originating from underside, just anterior to genital swellings. Endosoma forming irregular 3-dimensional mass produced into processes of varying size.

Final copepodid stage of male (from immature female on *H. fragilis*): body cyclopiform (Fig. 2A), total length 246  $\mu$ m, measured from tip of frontal process to posterior margin of caudal rami; maximum body width 80  $\mu$ m. Prosome comprising cephalosome plus 3 pedigerous somites: cephalosome with tapering frontal process (attachment structure of adult male) protruding through frontal margin just dorsal to base of rostrum. Rostrum (Fig. 2B) weakly developed, wider than long, with weakly concave tip. First urosomite bearing rigid seta at each posterolateral corner; second urosomite less than half length of anal somite. Anal somite elongate, about twice as long as wide and bearing paired caudal rami; each ramus about twice as long as wide and armed with 3 plumose setae.

Antennule 3-segmented (Fig. 2C), setal formula: 4 + ae, 1 + ae, 5 + ae. Antenna absent. Oral region located immediately behind rostrum on ventral surface of cephalosome; defined by complex arrangement of paired chitinous elements of obscure homology. Maxilliped (Fig. 2D) comprising short syncoxa, elongate basis and distal subchela consisting of unarmed endopodal segment plus long curved apical claw. Legs 1 to 3 biramous, coxae of each joined by intercoxal sclerite; basis unarmed, with protruding, rounded inner margin: legs 1 (Fig. 2E) and 2 each with 2-segmented exopod and 1-segmented endopod: first exopodal segment unarmed, second with 4 setae; endopod with 3 setae in both legs. Leg 3 (Fig. 2F) with 1-segmented rami: exopod with 4 setae, endopod with 2 setae. Leg 4 represented by single rigid seta at corner of first urosomite (Fig. 2A).

**Remarks**. The ovigerous females from *H. fragilis* are smaller than the material examined by Lützen (1964a) which typically had an ectosomal diameter in the range of 1.2 to 1.5 mm, although one specimen was 1.9 mm. Lützen did not report the host of his material although he noted that the most common host in northern Atlantic waters was *Harmothoe imbricata*. Lützen (1964a) also reported that the other known hosts included *H. extenuata*, *H. impar*, *Austrolaenilla mollis* and *Gattyana cirrhosa*. Two of the hosts reported here, *H. fragilis* and *Antinoe* sp., are new. This species has often been confused with *H. polynoes* but Lützen (1964a) unravelled the convoluted nomenclatural history and provided full synonymies for both species.

This species typically attaches to the side of the host in the anterior part of the body (commonly setigers 2 to 10 according to Lützen (1964a)), although O'Reilly *et al.* (2011) reported two females on the posterior setigers of *Gattyana cirrhosa*. The location on the host of the new material examined here varied from setiger 4 to setiger 20. A virtual horizontal section along a polychaete host infected with an *H. articus* reveals the extent of the endosoma located within the coelom of the host and visible on both sides of the gut (Fig. 4).

The final copepodid stage of the male enclosed a fully formed adult male (stippled in Fig. 2A) which was attached to the female by the tip of the frontal process extending out through an opening in the copepodid stage exuvium. This process is the "neck" of the bottle-shaped adult male. The paired spermatophores of the adult male were visible through the exuvium of the preceding copepodid and occupied most of the space within the prosome. The copepodid of *H. arcticus* is very similar to that of *H. polynoes* as figured by Lützen (1968). The setation of the apical segment of the antennule carries 4 setae plus an aesthetasc in the latter species (Lützen 1968, fig. 3b) compared to 5 setae plus an aesthetasc in *H. arcticus* (Fig. 2C). The segmentation and setation of legs 1 to 3 is the same in both species except Lützen (1968, fig. 3e) shows only 1 seta on the endopod of leg 2 whereas 3 are present in *H. arcticus*. These two minor setation differences may be the result of damage caused to the fragile setal elements during dissection.



**FIGURE 2**. Last male copepodid of *Herpyllobius arcticus* Steenstrup & Lütken, 1861 from female on *Harmothoe fragilis*. A, exuvium of last copepodid stage containing adult male (stippled), showing outline of spermatophores, dorsal; B, rostrum, ventral; C, antennule; D, maxilliped, E, leg 1 and intercoxal sclerite; F, leg 3 and intercoxal sclerite. Scale bars: A, 100 μm, B, D, 10 μm, C, E–F, 25 μm.

**Description of female from** *Harmothoe antilopes*: ectosoma of ovigerous female laterally compressed with deeply furrowed surface (Fig. 3A): anterior part of ectosoma narrowing and directed ventrally; posterior margin bearing large paired genital swellings (Fig. 3B). Ventral surface flattened; dorsal surface expanded and rounded. Cement glands paired, located laterally about in middle of body; gland strongly curved (Fig. 3A). Genital apertures about 320  $\mu$ m high and 194  $\mu$ m wide (Fig. 3B). Egg sacs multiseriate, cylindrical, about 948  $\mu$ m long and 500  $\mu$ m in diameter. Stalk about 112  $\mu$ m in diameter, located just posterior to mid-level of ectosoma. Endosoma (Fig. 3A) with basal mass extending into digitiform processes of different sizes; largest processes about 750  $\mu$ m in length.



**FIGURE 3**. *Herpyllobius arcticus* Steenstrup & Lütken, 1861 from *Harmothoe antilopes*. A, habitus of ovigerous female with male attached (arrowed), lateral view showing position of cement glands (dotted); B, ectosoma of female, posterior view showing attachment site of male (arrowed) dorsal to genital apertures; C, adult male containing paired spermatophores. Scale bars: A, 0.5 mm, B, 250 µm, C, 100 µm.

**Description of male from** *Harmothoe antilopes*: Adult male attached by means of frontal process to posterior surface of female, dorsal to genital apertures (arrowed in Fig. 3A, B). Body bottle-shaped (Fig. 3C), about 206  $\mu$ m in total length, comprising slender frontal process ("neck" of bottle) and rounded posterior part containing 2 spermatophores. Each spermatophore about 100  $\mu$ m long and 45  $\mu$ m in maximum width, with anteriorly directed tube extending towards frontal process.

**Remarks.** The single female from *H. antilopes* was attached laterally, close to the rear end of its host. It is ovigerous and has a bilaterally compressed ectosoma with a deeply-furrowed surface, suggesting that it had only recently extruded the paired egg sacs. The "spent" state of the female renders shape comparisons problematic. However, it differs from *H. polynoes* in its location on the host, since *H. polynoes* always attaches dorsally to the prostomium of its host (Lützen 1964a). This female has a broad stalk and a massive endosoma bearing digitiform processes whereas *H. polynoes* has a slender stalk and its endosoma is always flattened (Lützen 1964a). The other common species in Scandinavian waters is *H. arcticus* although this species rarely attaches to the posterior part of the host. This female is similar to *H. arcticus* in the form of the endosoma: its body length of about 1 mm is smaller than typical for *H. arcticus* but the difference might be due in part to its reproductive state. There are some differences such as the slightly larger diameter and slightly more anterior location of the stalk compared to typical *H. arcticus* (as redescribed by Lützen 1964a), However, all of these differences, as well as the relatively large size of the genital apertures of this specimen, could reflect the "spent" reproductive status of the female. Therefore, this female, despite its unusual location near the rear end of its host, is tentatively identified as *H. arcticus*.



**FIGURE 4**. A virtual horizontal section through polychaete host showing endosoma (arrowed) of adult female of *Herpyllobius arcticus* Steenstrup & Lütken, 1861 either side of host gut within coelomic cavity. Scale bar: 1 mm.

# Herpyllobius cluthensis sp. nov.

Syn: Herpyllobius polynoes: Chambers & Muir, 1997 (fig. 34)

**Type material**: Holotype ovigerous  $\bigcirc$  from *Malmgrenia andreapolis* McIntosh, 1874, Kingstone Hudds, Firth of Forth (55° 34.75'N, 02° 55.923'E), depth 40 m, 11 October 1991; collected by Lee Heaney (SEPA); NHMUK Reg. No. 2017.498. Paratype ovigerous  $\bigcirc$  from *Malmgrenia* sp., Loch Linnhe, Ardgour, Gorsten Fish Farm, Stn 4-2, depth unknown, 07 July 2004; collected by P.R. Garwood, NHMUK Reg. No. 2017.499. 2 paratype  $\bigcirc \bigcirc$  (1 ovigerous) on single host *M. andreapolis*, Firth of Clyde, Irvine Bay, Stn H (55° 35.9'N, 04° 47.40'E), depth 38 m, 19 April 2005; collected by M. O'Reilly (SEPA); NHMUK Reg. No. 2017.500.

Additional Material examined: 1 ovigerous  $\bigcirc$  on *Malmgrenia andreapolis*, Firth of Clyde, Irvine Bay, SEPA Stn Z, (55° 34.75'N, 04° 45.20'W), depth 40 m, 12 October 1979, figured in Chambers & Muir (1997) as *H. polynoes*, collection date of September 1981 cited in O'Reilly *et al.* (2011) is erroneous. 1 $\bigcirc$  on *M. andreapolis*, St. Abbs Sludge Disposal Grounds, Stn 13 (56° 04.50'N, 02° 07.25'W), depth 58 m, 02 June 1986. 2 ovigerous  $\bigcirc \bigcirc \bigcirc$  on single *M. andreapolis*, north Irish Sea, Block 112, (54° 38'N 04° 04'E), January 1998?, collected by Sue Hamilton

(specimen since lost). 1  $\bigcirc$  ovigerous on *M. andreapolis*, Firth of Clyde, Irvine Bay, SEPA Stn Z, (55° 34.75'N, 04° 45.20'W), depth 40 m, 19 April 2001. 1 ovigerous  $\bigcirc$ , on *M. andreapolis* Solway Firth, CSEMP Stn 25 (54° 44.97'N, 04° 00.22'W) depth 17.7 m, 04 November 2007. 1 $\bigcirc$  on *Malmgrenia arenicolae*, APEM Sample # 8460, Mourne Coast, EHS Stn ANA\_B, (54° 44.12'N, 05° 55.04'W), depth 19 m, 07 August 2013. 1 ovigerous  $\bigcirc$  on *Malmgrenia* sp., Western Isles, Isle of Harris, Meavaig Fish Farm, collected by P.R. Garwood, 2014? 1 ovigerous  $\bigcirc$  on *M. arenicolae*, Loch Nevis, collected by J. Hunter, 2015. NHMUK Reg. Nos 2018.122–127.



**FIGURE 5**. *Herpyllbius cluthensis* **sp. nov**. female. A, habitus of holotype female showing small ectosoma (viewed obliquely and appearing foreshortened) bearing paired egg sacs and bipartite endosoma comprising long proximal part and expanded apical part, with small ring of host tissue at penetration site; B, ectosoma of paratype female, dorsal view showing fragments of copepodid exuviae attached near posterior margin (arrowed); C, expanded apical part of endosoma of paratype female; D, paired genital apertures, ventral view. Scale bars: A, 1 mm, B–D, 0.5 mm.

**Differential diagnosis**. Ectosoma of adult female dorsoventrally flattened, with slightly concave undersurface (Fig. 5A), about 1.16 times wider than length along midline in dorsal view (Fig. 5B). Greatest width just posterior to middle of ectosoma (Fig. 5B). Mean ectosoma length 0.96 mm (based on 5 ovigerous specimens), range 0.77 to 1.10 mm, mean maximum width 1.11 mm, range 0.94 to 1.33 mm. Genital swellings located posteroventrally (Fig. 5D), moderately sclerotized, about 415 µm high by 360 µm wide. Stalk short, broad, originating anteroventrally at extreme anterior end of ectosoma. Endosoma (Fig. 5A, C) about 3.2 mm long, comprising long flattened proximal part terminating in flattened expanded apex, about twice width of proximal part; flattened apical part curved around gut of host. Egg sacs (Fig. 5A) multiseriate, up to 1.87 mm long (typically about as long as ectosoma). Male not found but fragments of last copepodid exuviae attached near mid posterior margin of female ectosoma (arrowed in Fig. 5B).

**Etymology**. The name of the new species refers to the locality, the Firth of Clyde, where the first specimen was found in 1979; it is a combination of *clutha*, which is the old name for the River Clyde, and *ensis* meaning from.

**Remarks**. The new species can be distinguished from its congeners in European waters by the shape of the ectosoma and by the extraordinary development of the flattened endosoma. The ectosoma is dorsoventrally flattened and slightly concave on the undersurface, and the stalk originates anteroventrally. It differs from *H. arcticus* which has a more globular ectosoma with the stalk originating on the underside, just anterior to genital swellings. The endosoma of *H. cluthensis* **sp. nov.** is elongate and flattened whereas that of *H. arcticus* is an irregular 3-dimensional mass produced into processes of varying size. In addition, the new species attaches to the head of its host whereas *H. arcticus* typically attaches to the side of the host in the anterior to middle part of the body (Lützen 1964a; present account).

*Herpyllobius polynoes* typically attaches to the head of its host (Lützen 1964a; present account) and the new species was also found attached to the head of its host. This shared attachment site has led to confusion between the two species. The specimen illustrated by Chambers & Muir (1997, fig. 34) as *H. polynoes* attached to *Malmgrenia andreapolis*, belongs to the new species, and is based on a sketch by M. O'Reilly of the first specimen found from Irvine Bay in 1979. Similarly we consider that the specimen from western Ireland figured by Gotto & O'Connor (1980) as *H. polynoes* from *Malmgrenia lunulata* (Delle Chiaje, 1830) probably belongs to the new species described here. O'Reilly (2011) had already reported on additional material of this copepod and commented that it may represent a new species. The two species can be readily distinguished: the ectosoma of the new species is wider than long, dorsoventrally flattened and the stalk originates anteroventrally, whereas in *H. polynoes* it is about 1.5 times longer than wide, strongly convex dorsally and the stalk originates in the posterior half. Both species have an elongate flattened endosoma but in *H. cluthensis* **sp. nov**. it has a flattened apical expansion, while in *H. polynoes* the endosoma tapers towards the apex.

Additional material of this species was found on *Malmgrenia andreapolis*, *M. arenicolae* (Saint-Joseph, 1888), and on unidentified *Malmgrenia* sp. Several other species of *Malmgrenia* occur in European seas, including newly described species (Barnich *et al.* 2017). It seems likely that *H. cluthensis* **sp. nov**. may occur on some of these. To date, its known distribution includes the Firth of Clyde, Firth of Forth, Solway Firth, Loch Nevis, Loch Linnhe, the Western Isles, the northern Irish Sea, the North Sea off St. Abbs, and possibly off western Ireland.

#### Herpyllobius cordiformis Lützen, 1964

#### Syn: Herpyllobius affinis: Stephensen, 1936

**Material examined**: 5 ovigerous  $\bigcirc \bigcirc \bigcirc$  from *Eunoe* cf. *oerstedi*, COPOL 1 (78° 57.3'N, 03° 34.8'E), depth 242 m, 02 October 2007; collected by A. Sikorski; NHMUK Reg. Nos 2015.2962-2965.

**Differential diagnosis.** Ectosoma of adult female subrectangular (Fig. 6D), tapering slightly anteriorly, in dorsal view, about 1.22 times longer than maximum width. Mean ectosoma length 2.56 mm (based on 5 specimens), range 2.40 to 2.76 mm, mean maximum width 2.10 mm, range 1.80 to 2.28 mm. Posterior end wider than anterior and bearing conspicuous median posterior lobe about 300  $\mu$ m in diameter (arrowed in Fig. 6C, D) on posterior margin, located on midline between and just dorsal to paired genital openings. Genital swellings prominent (Fig. 6D), heavily sclerotized, about 640  $\mu$ m high by 425  $\mu$ m wide. Stalk short, broad, originating on underside of ectosoma almost beneath genital apertures. Endosoma forming irregular mass with numerous small,

flattened lobate processes around margins. Egg sacs (Fig. 6C) elongate, slightly curved, multiseriate, up to 5.46 mm long (twice as long as ectosoma).



**FIGURE 6**. *Herpyllobius polynoes* (Krøyer, 1864). A, habitus of ovigerous female, posterior view with swelling in midline arrowed; B, ectosoma, lateral. *Herpyllobius cordiformis* Lützen, 1964. C, habitus of ovigerous female, lateral view with median posterior lobe arrowed; D, ectosoma of female, dorsal. All scale bars 1 mm.

**Remarks**. Three of the females in this sample were already detached from the host but two were still attached to parapodia with the lobate endosoma extending towards the body of the host. These are large parasites: the new material is up to 2.76 mm in ectosomal length with slightly curved egg sacs up to 5.46 mm long. However, this is smaller than the material described by Lützen (1964a). The female from Cape Elisabeth in Maine, figured by Lützen (1964a, fig. 13), was 3.5 mm long with egg sacs about 4.1 mm long, but he also reported a female from "a giant specimen" of *Eunoe nodosa* which was 4.5 mm long and had egg sacs up to 12 mm in length. This species appears somewhat variable in size, perhaps dependent in part upon host species. Despite this difference in body size, the material from *Eunoe* cf. *oerstedi* is identified as *H. cordiformis* due to the possession of the conspicuous rounded median posterior lobe located just dorsal to the genital apertures, a unique feature among *Herpyllobius* species, combined with the extreme posterior location of the stalk, which originates almost beneath the genital apertures (Fig. 6C).

This species was originally described based on material from the Atlantic coast of Maine (USA) on the host *Nychia cerosa* (probably *Gattyana cirrhosa*, according to Lützen (1964a)) and from Greenland on *Eunoe nodosa* (Lützen 1964b). In addition, the material from Inglefield Bay, Greenland, identified by Stephensen (1936) as *Herpyllobius affinis* Hansen, 1887, was considered to belong to *H. cordiformis* by Lützen (1964a). This is the first record from European waters and, at 78°N, is located well into the Arctic Circle.

# Herpyllobius polynoes (Krøyer, 1864)

Syn: Silenium polynoes Krøyer, 1864 Herpyllobius affinis Hansen, 1887

Norwegian material examined: 3  $\bigcirc$  dorsally on prostomium of 3 specimens of *Harmothoe imbricata*, 3566 Nessar, Hopen Bank Top Stn 11 (76° 06.98'N, 23° 52.10'E), depth 56 m, 01 October 2009; collected by A. Sikorski; NHMUK Reg. No. 2015.2968-2970. 19 dorsally on prostomium of Harmothoe cf. imbricata, Barents Sea, Spitsbergen Bank Stn 11-5 (76° 07.00'N, 23° 51.3'E), depth 56 m, 08 August 1992; collected by A. Sikorski. NHMUK Reg. No. 2015.2966. 19 dorsally on prostomium of Harmothoe imbricata, Nessar 2007, Hopen Bank Top Stn 11 (76° 07.40'N, 23° 53.23'E), depth 60 m, 17 August 2007; collected by A. Sikorski. NHMUK Reg. No. 2017.172. 1 $\bigcirc$  dorsally on prostomium of *H. imbricata*, no locality data; collected by A. Sikorski; used for SEM. 1♀ dorsally on prostomium of *Harmothoe bifera*, Mareano Bomtrål, Stn 821-16, depth unknown, 08 May 2012; collected by A. Sikorski; NHMUK Reg. No. 2015.2967. 1 $\bigcirc$  with 2  $\bigcirc$  attached, dorsally on prostomium of Malmgreniella mcintoshi (Tebble & Chambers, 1982), Mareano 2010110, Stn 624-373, depth unknown, 21 September 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.2971. 1 immature Q dorsally on prostomium of M. mcintoshi, Mareano Bomtrål, Stn 870-27, depth unknown, 10 October 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.2972.  $2 \bigcirc \bigcirc$  dorsally on prostomium of *Eunoe ?barbata*, H1-Trål, North Cape Bank, Stn Brønn (72.01°N 25.3°W), depth 245 m; 15 August 2007; collected by A. Sikorski; NHMUK Reg. No. 2015.2973.  $2\Im$  dorsally on prostomium of 2 specimens of *Eunoe nodosa*, 3703 Mareano 2013, Stn 1218-471, depth unknown, 17 August 2013; collected by A. Sikorski; NHMUK Reg. No. 2016.543-544. 299 dorsally on prostomium of E. nodosa, 7018 Melkøya 2014, Stn 3-2 (70.67405°N 23.60273°E), depth 115 m; 12 August 2014; collected by A. Sikorski; NHMUK Reg. Nos 2017.170-171.

**British material examined**: 1 ovigerous  $\bigcirc$  from *Gattyana cirrhosa* (also with an ovigerous  $\bigcirc$  of another copepod, *Selioides bocqueti*, attached dorsally behind the host head), St. Abbs Sludge Disposal Grounds, Stn1 (56° 06.50'N, 02° 07.25'W), depth 51 m, 16 June 1992. 1 ovigerous  $\bigcirc$  from *G. cirrhosa*, (also with  $\bigcirc$  *Selioides bocqueti*) Northumberland coast, Stn 20, 05 May 1993; collected by P. Garwood (see O'Reilly & Geddes 2000); NHMUK Reg. No. 2017.480. 1  $\bigcirc$  from *G. cirrhosa*, Northumberland coast, Stn 47, 04 June 1993; collected by P. Garwood (see O'Reilly & Geddes 2000). 1  $\bigcirc$  from *Harmothoe antilopes*, Firth of Clyde, Garroch Head, SEPA Stn T7.1 (55° 38.82'N, 04° 01.45'W), depth 139 m, 9 November 2000. 1 ovigerous  $\bigcirc$  from *G. cirrhosa*, Firth of Clyde, Cloch Point, Stn CMT7 (55° 56.85'N, 04° 53.65'W), depth 80 m, 13 April 2004. 3  $\bigcirc$  (1 ovigerous) from single *G. cirrhosa*, Loch Striven, Ardyne Point Fish Farm, Stn R1-1 (55° 53.218'N, 05° 03.336'W), depth 40 m, 24 August 2006; collected by J. Richard. 1 $\bigcirc$  (+ 2 $\bigcirc$  $\bigcirc$ ), 1 immature  $\bigcirc$  (+ 10 $\bigcirc$  $\bigcirc$ ), 1 immature  $\bigcirc$  (+ 2 $\bigcirc$  $\bigcirc$ ), from single *G. cirrhosa*, ATL 1.3 FB (locality data unknown); collected by P. R. Garwood. 1 $\bigcirc$  from *G. cirrhosa*, ATL 1.6 FB

(locality data unknown); collected by P. R. Garwood.  $1^{\circ}$  from *G. cirrhosa*, Blyth, ENTEC, Stn 41 (locality data unknown), collected by P. R. Garwood. NHMUK Reg. Nos 2018.128-133.



**FIGURE** 7. Scanning electron micrographs of *Herpyllobius polynoes* (Krøyer, 1864). A, ectosoma of female attached to host, dorsal; B, same, posterior view showing genital apertures. Scanning electron micrographs of *Eurysilenium truncatum* M. Sars, 1870. C, ectosoma of female attached adjacent to elytrophore of host, dorsal; D, same, showing incomplete male attached posteriorly (arrowed). Scale bars: A–C, 0.5 mm, D, 200 µm.

**Differential diagnosis**. Adult female ectosoma (Fig. 7A, B) about 1.5 times longer than wide and often slightly pointed posteriorly; underside flat, or slightly concave; dorsal surface sometimes humped near middle. Genital swellings prominent. Small median swelling located on posterior surface dorsal to genital apertures; four

minute sclerotized dots arranged in arc dorsal to median swelling. Stalk short, slender, originating from underside about one third to half of ectosoma length anterior to genital swellings. Endosoma flattened, 2 to 3 times longer than ectosoma (e.g. female with ectosoma 1.86 mm in length, with endosoma 5.8 mm long).

**Description of Female from** *Eunoe ?barbata*: Ectosoma of adult female slightly pointed at anterior end and humped in mid-dorsal surface (Fig. 6A, B). Ectosomal length 1.50 mm, about 1.7 times longer than maximum width. Genital swellings (Fig. 6A) prominent, moderately sclerotized; genital apertures about 310  $\mu$ m high by 240  $\mu$ m wide, separated by gap of about 180  $\mu$ m. Small swelling located in mid-line between and just dorsal to genital swellings (arrowed in Fig. 6A); four minute sclerotized dots arranged in arc dorsal to median swelling. Stalk short, about 100–105  $\mu$ m in diameter, originating on underside of ectosoma close to mid-body. Endosoma elongate, in form of flattened lobe 3.27 mm in length and 0.60 mm in maximum width, with simple margins. Egg sacs pear-shaped (Fig. 6A), up to 1.45 mm long by 1.0 mm wide, eggs multiseriate, about 80  $\mu$ m in diameter.

**Remarks**. According to Lützen (1964a) this species always attaches dorsally on the prostomium of its host (Fig. 5A). In northern Atlantic waters, its predominant host is *Harmothoe imbricata* but its known host range includes *Austrolaenilla mollis*, *Bylgides promamme*, *B. sarsi*, *Eunoe nodosa*, *Gattyana amondseni*, *G. cirrhosa*, *Gaudichaudius iphionelloides*, *Harmothoe aspera*, *H. extenuata*, and *H. impar* (see Boxshall & Halsey 2004). In UK waters the predominant host is *G. cirrhosa* (O'Reilly 1999; O'Reilly & Geddes 2000; O'Reilly *et al.* 2011) but it also been reported on *H. antilopes* (O'Reilly *et al.* 2011). Three of the hosts recorded here, *Harmothoe bifera*, *Malmgreniella mcintoshi* and *Eunoe ?barbata* are new hosts for *H. polynoes*. All known hosts of *H. polynoes* are members of the subfamily Polynoinae. *Herpyllobius polynoes* may co-occur on the same host specimen with the herpyllobiid copepod *Eurysilenium truncatum* (see O'Reilly *et al.*, 2011) or with the nereicolid copepod *Selioides bocqueti* (this paper and O'Reilly & Geddes, 2000).

The sole female from *Eunoe ?barbata* was attached to the dorsal surface of the prostomium of its host, with its paired genital apertures and eggs sacs directed anteriorly. This is the classic site for *H. polynoes* according to Lützen (1964a). The endosoma of this female extended anteriorly into the everted proboscis of the host. The characteristic arrangement of four "sclerotized dots" in an arc dorsal to the median swelling, highlighted as a feature of *H. polynoes* by Lützen (1964a) can be difficult to observe in preserved material. They were visible in the female from *Eunoe ?barbata* only after it had been cleared in lactic acid and SEM images of a female from *Harmothoe imbricata* clearly show the median swelling (Fig. 6B) but not the sclerotized dots. Lützen (1966) stated that these dots are cuticular thickenings although he noted that, in one large specimen of *H. polynoes* minute ducts from unicellular subsurface glands opened on them.

The ventral stalk connecting ectosoma and endosoma is located near the middle of the ectosoma in the female from *Eunoe ?barbata*. This is slightly more anteriorly placed than the typical position, about one third of the ectosoma length anterior to the genital swellings (Lützen 1964a), but the shared possession of other features discussed above and the location on the prostomium of the host, support the identification of this parasite as *H. polynoes*.

# Genus *Eurysilenium* M. Sars, 1870

**Diagnosis**. Adult female ectosoma angular, bilaterally symmetrical, with inconspicuous genital swellings. Genital apertures transverse, slit-like, located ventrally on swellings at or near posterior margin of ectosoma. Stalk originating on flattened underside of ectosoma, distinctly in anterior half of body. Endosoma circular in cross-section and tapering gradually towards bulbous tip; typically looped around gut of host. Egg sacs curved, multiseriate. Adult male oblong, tapering posteriorly, indistinctly 6-segmented, comprising cephalothorax and 5 more-or-less well defined trunk somites; fourth trunk somite with paired, ventrally-directed lobate swellings; fifth (anal) somite bearing elongate caudal rami, hooked at tip. Single pair of stylet-like structures present in oral region.

Type species: Eurysilenium truncatum M. Sars, 1870, by monotypy.

**Remarks**. There are currently five valid species in the genus *Eurysilenium*: *E. truncatum*, *E. australis* López-González, Bresciani & Conradi, 2006, *E. fungosum* Stock, 1996, *E. intermedium* Stock, 1986, and *E. oblongum* Hansen, 1887. All species occur on polynoid worms. Only *E. truncatum* has been commonly reported from European waters, from southern Norway and Sweden, the Skagerrak and Kattegat (Lützen 1964a, 1966, 1968), and Scotland (O'Reilly *et al.* 2011). The known distribution of *E. oblongum* ranges from Labrador and

Greenland in the west to the Kara Sea in the east (Lützen 1964a). The remaining species are reported from New Caledonia (*E. intermedium*), Indonesia (*E. fungosum*), and Antarctica (*E. australis*) (Stock 1986, 1996; López-González *et al.* 2006). The name *E. antarcticum* used by López-González *et al.* (2006: p. 258) is presumably a *lapsus*. The male of *E. australis* was described in detail using both light and scanning electron microscopy by López-González *et al.* (2006).

# Eurysilenium truncatum M. Sars, 1870

Scandinavian material examined:  $3 \bigcirc \bigcirc$  from *Eucranta villosa* Malmgren, 1866, Snorre TLP/UPA, Stn 24-5 (61.48564°N, 02.231242°E), depth 332 m, 07 June 2005; collected by A. Sikorski; NHMUK Reg. No. 2013.147-148,  $1\bigcirc$  used for SEM.  $1\bigcirc$  from *E. villosa*, 3940 Arenaria 2, Stn 1-4 (72.63017°N, 24.92828°E), depth 270 m, 24 June 2007; collected by A. Sikorski; NHMUK Reg. No. 2015.2998.  $1\bigcirc$  from *E. villosa*, Snøhvit N, Stn 13-2 (71.49036°N, 21.07921°E), depth 329 m, 19 June 2007; collected by A. Sikorski; NHMUK Reg. No. 2015.2999.  $1\bigcirc$  from *Eunone* sp., Troll B, Stn 44-4 (60.7108°N, 03.5100671°E), depth 322 m, 27 May 2001; collected by A. Sikorski; NHMUK Reg. No. 2015.3000.  $3\bigcirc \bigcirc$  (2 ovigerous) from *G. cirrhosa*, SW of Yttre Vattenholmen, Kosterfjord, Sweden, depth unknown, 27 August 1986; collected by A. Mackie. Deposited National Museum of Wales, Reg No. NMWZ 1986.108.44. 1 ovigerous  $\bigcirc$  from *G. cirrhosa*, SW of Yttre Vattenholm, Kosterfjord, Sweden, depth 60-80 m, 28 October 1989; collected by A. Mackie, Deposited National Museum of Wales, Reg No. NMWZ 1986.108.44.

**British material examined:** 1 ovigerous  $\bigcirc$  from *G. cirrhosa*, East Shetland Basin, Stn 90, (60°34.49'N, 01°21.33'W) depth 136 m, 25 July 2007; collected by P.R. Garwood. NHMUK Reg. No. 2017.479. 1 mature  $\bigcirc$  and 5 juvenile  $\bigcirc$  attached to single *G. cirrhosa*, Isle of Mull, Loch Scridain, SEPA Stn 22 (55°21.14'N, 06°59.53'W), depth 26 m, 24 May 2016. NHMUK Reg. No. 2018.134.

**Differential diagnosis.** Ectosoma of adult female subrectangular in outline, with anterior margin produced anterolaterally into paired lobate shoulders (Figs 7C, D, 8B, C). Lateral margins irregular, tapering slightly posteriorly (Figs 7D, 8C). Length of ectosoma ranging from 0.73 mm to 1.2 mm, and width ranging from 0.80 mm to 1.48 mm. Posterior margin of ectosoma straight to weakly rounded. Ectosoma dorsoventrally flattened, with paired genital apertures located ventrally close to posterior margin and either side of mid-line. Genital apertures slit-like, with sclerotized opercular plates anterior and posterior to slit (Fig. 8C). Egg sacs curved (reniform), directed laterally, eggs multiseriate. Stalk originating from flat underside in midline and in anterior quarter to third of ectosoma. Endosoma (Fig. 8A) elongate, typically 5 to 6 mm in length in adult female, circular in cross-section and tapering distally, terminating in globular swelling; typically looping around gut.

Male (Fig. 8E) about 250 µm in total body length excluding caudal rami; body indistinctly segmented, tapering posteriorly, comprising well-defined, subrectangular cephalothorax and indistinctly 4- or 5-segmented post-cephalothoracic trunk. Penultimate trunk somite with paired lobate appendages located ventrally. Anal somite bearing paired elongate caudal rami, each distinctly hooked at tip; rounded lobes present lateral to bases of caudal rami. Cephalothorax attached to female by ventral surface. Single pair of stylet-like structures present, either side of midline, in oral region anterior to mid-length of cephalothorax.

**Remarks**. The original description of the male of *E. truncatum* suggested that the male was attached to the female by a sticky secretion and no mouthparts were noted (M. Sars 1870; Lützen 1964a). The male of *E. truncatum* described here was attached to the female between the genital apertures. The attachment interface was the ventral surface of the cephalothorax and a secretion may have been involved, but paired stylets were also present in the oral region, as described for *E. oblongum* by Lützen (1964a). These stylets presumably represent modified mouthparts. The body length of the male given by Lützen (1964a) was 250 µm excluding the caudal rami. López-González *et al.* (2006) described male *E. australis* as possessing an elongate body, tapering posteriorly, indistinctly segmented, limbless, and with hooked caudal rami posteriorly. On the ventral surface of the cephalothorax they described two "pairs of denticulated triangular elements", a "pair of marginal bifid elements" and a "pair of tubular flaccid tubes that could be interpreted as spermiducts (?)", plus a pecten-like area of uncertain homology in the mid-line. López-González *et al.* (2006) reported more paired structures than any previous study but did not offer any interpretations of the homology of these structures. As a generalization, it appears that males of *Eurysilenium* attach to the female by the ventral surface of the cephalothorax, and that this surface is provided



**FIGURE 8**. *Eurysilenium truncatum* M. Sars, 1870. A, detached endosoma of female from *Eucranta villosa*; B, ectosoma of ovigerous female from *Eunone* sp., dorsal, with cephalothorax of attached male (arrowed) just visible between genital apertures of female; C, same, ventral view with male removed; D, curved egg sac detached from female from *Eunone* sp.; E, genital apertures of female with male attached, ventral. Scale bars: A, 1.0 mm, B–D, 0.5 mm, E, 200 µm.

with vestiges of at least one pair of appendages. López-González *et al.* (2006) interpreted the posterior-most pair of these structures (the flaccid tubes) as "spermiducts". Presumably they are suggesting that these ducts represent spermatophore tubules through which the contents of the spermatophores will eventually discharge, as described for *Herpyllobius* males by Lützen (1966). López-González *et al.* (2006) similarly described paired pores that they attributed to the "spermiducts", in the scar where the cephalothorax of the male of *Gottoniella antarctica* López-González, Bresciani & Conradi, 2006 was attached to the female. This implies that males of *Eurysilenium* and *Gottoniella* discharge their spermatophore contents anteriorly via their cephalothoracic attachment onto the female, as in *Herpyllobius*, rather than posteriorly via paired genital apertures on the urosome, as is typical of the vast majority of copepods.

The original host of *E. truncatum* listed by Sars (1870) was *Harmothoe imbricata* (as *Polynoe cirrata*), but according to Lützen (1964a) the most common host is *Gattyana cirrhosa*. Lützen (1964a) also noted that *E. truncatum* was invariably attached to the dorsal surface of the host in mid-body, typically between setigers 8 and 15. The three adult females reported from a single individual of *Eucranta villosa* (collected off the coast of southern Norway) were attached on setigers 14, 18 (Fig. 8C) and 25 of a single host. The parasites are typically concealed beneath the elytra of the host.

This species has been reported from numerous locations around southern Norway and into the Skagerrak and Kattegat (Lützen 1964a), and from Scotland, off Shetland and in the Firth of Clyde in Scotland (O'Reilly *et al.* 2011). The depth range recorded in the present account for material of this species from Scandinavian waters was 270 to 332 m whereas in Scottish waters it occurs as shallow as 26–80 m. The record here of *E. truncatum* on *Eucranta villosa* collected at 72.6°N is the most northerly record to date and is the first from this host.

# Eurysilenium sp.

**Material examined**: 1 $\bigcirc$  (non-ovigerous) from *Harmothoe fragilis*, Vigdis, Stn 9-2 (61.3783°N, 02.104723°E), depth 281 m, 11 June 2005; collected by A. Sikorski; NHMUK Reg. No. 2016.545. 1 ovigerous  $\bigcirc$  and 1 mature  $\bigcirc$  attached dorsally on single *Harmothoe impar*, Fladden Stn 72 (58.063°N 0.550°E), depth 152 m, collected by J.P. Hartley, 23 November 2015. 2 ovigerous  $\bigcirc \bigcirc \bigcirc \bigcirc$  (1 with 2 dwarf males attached) located dorsally on *H. impar*, Fladden Stn 82 (58.351°N 1.218°E) depth 133 m, collected by J.P. Hartley, 23 November 2015. NHMUK Reg. Nos 2018.135-138.

**Differential diagnosis.** Ectosoma of adult female from *H. fragilis* dorsoventrally flattened, heart-shaped in outline, with anterior margin weakly produced anterolaterally into paired lobate shoulders (Fig. 9A). Lateral margins of ectosoma converging posteriorly; posterior margin rounded. Length of ectosoma 1.11 mm, width 1.46 mm. Ectosoma with paired genital apertures located ventrally on posterior surface, either side of mid-line. Genital apertures slit-like, with sclerotized opercular plates anterior to slit and narrow sclerotized bar posterior to slit (Fig. 9A). Egg sacs unknown. Stalk originating from flat underside in midline, in anterior quarter of ectosoma. Endosoma elongate, circular in cross-section and tapering distally, terminating in globular swelling.

Male small, about 185  $\mu$ m in total body length including caudal rami, 165  $\mu$ m excluding caudal rami; maximum width about 65  $\mu$ m; body indistinctly 6-segmented (Fig. 9B), tapering posteriorly, comprising well-defined, subrectangular cephalothorax and 5-segmented post-cephalothoracic trunk. Fourth trunk somite with paired lobate swellings ventrally. Anal somite bearing paired elongate caudal rami, each distinctly hooked at tip; rounded lobes present on somite lateral to bases of caudal rami. Cephalothorax attached to female by ventral surface; with trace of rostrum mid-ventrally in frontal region. Single pair of stylet-like structures present, either side of midline and anterior to mid-length of cephalothorax.

**Remarks**. The ectosoma of the female from *H. fragilis* is heart-shaped whereas that of typical *E. truncatum* (Fig. 8B, C) is more rectangular with its lateral margins tapering only slightly. There are also differences in the position and shape of the genital apertures: they are more posteriorly located in *E. truncatum* than in the female from *H. fragilis*, and the relative sizes of the anterior and posterior plates framing the slit-like genital openings are different. In the female from *H. fragilis* the posterior plates are more bar-like compared to the deeper plates of *E. truncatum*. However, we have only a single female from *H. fragilis*. There is an additional difference in the male: the body length of the male attached to the female from *H. fragilis* is 165 µm, excluding the caudal rami, which is smaller than the 250 µm reported for the male of *E. truncatum* here and by Lützen (1964a).



**FIGURE 9**. *Eurysilenium* sp. from *Harmothoe fragilis*. A, ectosoma of female, ventral showing male attached between ventrally-located genital apertures of female; B, adult male, dorsal. Scale bars: A, 0.5 mm, B, 100 µm.

The *Eurysilenium* material from *H. impar* has more strongly produced anterolateral lobes than the material from *H. fragilis* and tapers more strongly towards the rear. Such variability in form of the ectosoma has been apparent in *E. truncatum* right from the original description, in which Sars (1870) figured two ovigerous females; one with a heart-shaped ectosoma bearing spherical egg sacs and the other with large anterolateral lobes, more strongly tapering lateral margins on the ectosoma, and bearing kidney-shaped egg sacs attached eccentrically (cf. Sars 1870, figs 16 and 17). These two syntypes look remarkably different from each other.

It is difficult to interpret such differences. It is clear that in herpyllobiids the shape of the ectosoma of the adult female can vary markedly according to their individual reproductive state, so it is unlikely to be reliably diagnostic of species identity. So, despite these differences noted above in material from particular hosts, it will be necessary to obtain more data, preferably including molecular sequence data, before the taxonomic significance of these differences in ectosomal shape can be ascertained.

The females from *H. impar* are located dorsally on their hosts, attached between setigers R11 and R15. Their ectosomas are orientated at right angles to the host, with the posterior end directed outwards.

#### Family Pholoicolidae fam. nov.

The diagnosis of the new family corresponds with the diagnosis of the only genus given below.

#### Genus Pholoicola gen. nov.

**Diagnosis**. Adult female highly transformed and deeply embedded in host with only tip of genitoabdomen protruding through host's body wall. Body bipartite (Fig. 10A, B) comprising large anterior part separated from narrower, tapering posterior genitoabdomen by deep furrow. Anterior part trilobate, with median frontal lobe and paired dorsolateral lobes, containing ovaries, and varying in size with reproductive state of individual female. Genitoabdomen widest at origin on ventral surface of anterior part, narrowing gradually toward rounded posterior extremity bearing paired genital apertures ventrally. Asymmetrical dorsolateral lobes present on genitoabdomen.



**FIGURE 10**. *Pholoicola chambersae* **gen. et sp. nov**. A, adult female with 3 males attached, ventral; B, female, dorsal; C, detached egg sac; D, adult male, lateral view showing position of developing paired spermatophores; E, adult male, ventral; F, cephalothorax of male, lateral view showing thickened frontal region and clawed limb; G, spermatophore; H, last male copepodid stage, antennule; I, antenna; J, maxilliped. Scale bars: A, 0.5 mm, B–C, 250 μm, D–E, 50 μm, F–H, 25 μm, I–J 10 μm.

Conspicuous paired oviducts located within tapering genitoabdomen. No vestiges of any limbs observed; caudal rami lacking; without anus. Egg sacs paired, subspherical (Fig. 10C); attached as orientated in Figs 10B–C.

Adult male body about 122  $\mu$ m in total length; comprising cephalothorax and ovoid post-cephalothoracic trunk (Fig. 10D, E) set at angle to each other. Cephalothorax produced anteriorly into rectangular frontal zone. Single pair of reduced cephalothoracic limbs present, located ventrolaterally on frontal zone; each limb armed with short apical claw. Spermatophore sausage-shaped with long slender sperm tube, attached to body surface of female, adjacent to genital apertures.

Last male copepodid: antennule 5-segmented with aesthetascs on segments 2, 4, and 5; antenna comprising 2 slender segments plus slender apical claw; maxilliped subchelate, comprising small syncoxa, robust basis and slender subchela consisting of proximal endopodal segment plus terminal claw.

Type species: Pholoicola chambersae gen. et sp. nov., by original designation.

**Etymology**. The name of the new genus is based on *Pholoe*, the name of the host genus, plus *–icola*, meaning inhabitant: gender masculine.

**Remarks.** This genus differs in its fundamental organization from the Herpyllobiidae, Bradophilidae, Phyllodicolidae, and Saccopsidae. Almost the entire body of the transformed adult female is embedded in the host, forming the large lobate endosoma, so that only the tapering genitoabdomen, bearing the paired genital apertures, extrudes through the host's body wall. The ovaries lie within the main body, with only the oviducts inside the tapering genitoabdomen and the genital apertures located externally at its tip. This body plan differs from the four families listed above, in all of which the endosoma and ectosoma are connected by a well-defined stalk that passes through the host body wall, and in which the ovaries are entirely contained within the ectosoma. Almost the entire body of female *Pholoicola* gen. nov. is located within the host and there is no defined stalk. It is possible that the anterior trilobate part represents an ancestral endosoma and the posterior genitoabdomen represents an ancestral ectosoma, in which case the constriction between these two parts would represent the original stalk, but more detailed anatomical studies are necessary before any such system of homologies can be robustly established. There is an important difference between the last male copepodid stage of *Pholicola* gen. nov. and the herpyllobiids, namely that it retains a clawed antenna located adjacent to the base of the antennule. There is no trace of an antenna in the male copepodids of herpyllobiids (Lützen 1968).

The new genus exhibits some similarities to the recently established Jasmineiricolidae in which the embedded endosoma is much larger than the ectosoma and contains the ovaries, and there is no defined stalk (Boxshall *et al.* 2015). However, the Pholoicolidae differs from the Jasmineiricolidae in the lack of a functional anus, in the lack of subchelate maxillipeds in the adult female and in the lack of the rosette-like array of eight slender lobes on the ventral surface of the cephalothorax, which are probably derived from the mouthparts. The ovaries of the *Pholoicola* gen. nov. are located anteriorly, close to the constriction where the tapering genitoabdomen merges with the endosoma, whereas in the Jasmineiricolidae the ovaries are located anterolaterally within the postcephalic trunk and lateral trunk lobes.

The male of *Pholoicola* gen. nov. is highly reduced. The paired limbs retained by the male are probably the antennae, given their frontal position on the cephalothorax and their subchelate structure. They appear to be used to secure the male to the female. We did not find any males containing spermatophores ready for deposition. However, a pair of early developing spermatophores containing packed filiform sperm, was located in the cephalothorax and anterior part of trunk, and we consider it likely that the spermatophores are deposited anteriorly (as in *Herpyllobius*).

#### Pholoicola chambersae gen. et sp. nov.

**Type material:** Holotype  $\bigcirc$  and 2 paratype ovigerous  $\bigcirc \bigcirc \bigcirc$  from single *Pholoe pallida* Chambers, 1985, Fram V, Stn A2 5-5 (61.0884°N, 03.5091°E), depth 357 m, 04 June 2004; collected by A. Sikorski; NHMUK Reg. No. 2016.546 (Holotype on setiger 11 on right side) and 2016.547-548 (paratypes on setigers 25 and 33 on left side). 2 ovigerous paratype  $\bigcirc \bigcirc$  from 2 specimens of *P. pallida*, 4315 Loshavn, Stn 7-4 (57.6122°N, 06.604321°E), depth 172 m, 27 May 2008; collected by A. Sikorski; NHMUK Reg. No. 2016.549-550. 2 paratype  $\bigcirc \bigcirc$  from single *P. pallida*, Troll B, Stn 12-4 (60.7288°N, 03.664°E), depth 312 m, 02 June 2004; collected by A. Sikorski. NHMUK Reg. No. 2017.162. 3 paratype  $\bigcirc \bigcirc (1 \text{ ovigerous})$  from single *P. pallida*, 8690 Saltkjevika C, Stn Salt 3-2 (64°

35.909'N, 11° 16.572'E), depth 244 m, 05 January 2017; collected by A. Sikorski; NHMUK Reg. Nos 2017.163-165.

**Differential diagnosis**. Adult female highly transformed and deeply embedded in host with only genitoabdomen protruding through body wall of host. Body length about 0.56 mm. Body bipartite (Fig. 10A, B) comprising large anterior part separated from narrower, tapering posterior genitoabdomen by deep furrow. Anterior part trilobate, with median frontal lobe and paired dorsolateral lobes; varying in size with reproductive state of female, maximum width about 0.6 mm. Genitoabdomen about 0.37 mm long, widest at origin on ventral surface of anterior part, narrowing gradually toward rounded posterior extremity, bearing paired genital apertures ventrally. Asymmetrical dorsolateral lobes present on genitoabdomen (Fig. 10B). Ovaries and paired oviducts located within embedded genitoabdomen. No vestiges of any limbs observed; caudal rami lacking; without anus. Egg sacs paired, subspherical (Fig. 10C), about 250 um in diameter; eggs about 80 µm in diameter.

Adult male mean body length 128  $\mu$ m (range 122 to 135  $\mu$ m, based on 4 specimens); comprising cephalothorax and ovoid post-cephalothoracic trunk (Fig. 10D, E); cephalothorax about 54  $\mu$ m in width, deflected ventrally at angle to trunk (Fig. 10D); produced anteriorly into thickened rectangular frontal zone about 22  $\mu$ m wide (Fig. 10F). Single pair of reduced cephalothoracic limbs present, located ventrolaterally on protruding frontal zone; each limb armed with short apical claw. Spermatophore sausage-shaped (Fig. 10G), about 50  $\mu$ m long by 15  $\mu$ m wide, with long slender sperm tube. Paired developing spermatophores visible within male (Fig. 10D), located anteriorly within cephalothorax and anterior part of trunk; containing elongate filiform sperm.

Final copepodid of male: antennule 5-segmented (Fig. 10H); setation 1, 5 + ae, 1, 2 + ae, 4 + ae. Antenna originating adjacent to base of antennule; comprising 2 slender segments plus slender apical claw (Fig. 10I). Maxilliped subchelate (Fig. 10J), comprising small syncoxa, robust basis and slender subchela consisting of unarmed proximal endopodal segment and second segment armed with inner seta and fused to terminal claw. Other features of copepodid stage unknown.

**Etymology**. The new species is named in honour of Sue Chambers, the discoverer of the only known host of this parasite.

**Remarks**. We did not find a complete copepodid stage but on several occasions males were associated with the extreme anterior end of the moulted final copepodid exuvium which had become trapped between the attached male and the female. The antennule was 5-segmented and its setation pattern, with large aesthetascs on segments 2, 4 and 5 is shared with *Eurysilenium* as figured by Lützen (1968). The segmentation of the maxilliped (Fig. 10J) of *P. chambersae* gen. et sp. nov. is the same as that found in the final copepodid stage of herpyllobiids: in both *Herpyllobius arcticus* (cf. Fig. 2D) and *Eurysilenium australis* (see López-González *et al.* 2006) the subchela comprises two endopodal segments with the second fused to the terminal claw; the second segment is armed with an additional seta in *E. australis* and *Pholoicola* gen. nov. but this seta is lacking in *H. arcticus*.

The only known host is the pholoid *Pholoe pallida* and this is the first parasitic copepod to be reported from any member of the family Pholoidae. It is reported here from off the west coast of Norway between 57° and 64°N and its known depth range is 172 to 357 m. The females are typically embedded in the side of the host and the tip of the female genitoabdomen protrudes through the lateral body wall of the host between adjacent parapodia. The females are commonly attached in the mid-body region, but were found in positions ranging from setiger 6 to setiger 33.

# Family Phyllodicolidae Delamare Deboutteville & Laubier, 1961

The family name is a replacement for Phyllocolidae Delamare Deboutteville & Laubier, 1960 which was based on a preoccupied generic name, *Phyllocola* Delamare Deboutteville & Laubier, 1960. The family Phyllodicolidae comprises two genera and three species are currently known; all are mesoparasites of phyllodocid polychaetes (O'Reilly 2000). The endosoma of the adult female has the form of paired buccal rhizoids that penetrate the host's coelom. Various developmental stages of females have been reported (Laubier 1961; Gotto & Leahy 1988), but no males, and the family has thus far been recorded only from the North Atlantic and Mediterranean. The family currently comprises two genera, *Phyllodicola* Delamare Deboutteville & Laubier, 1961 and *Cyclorhiza* Heegaard, 1942, but it is difficult to identify robust characters to separate these genera. Their validity as distinct genera is in need of re-assessment but the lack of any information concerning males in this family is a significant obstacle to such a revision.

#### Genus Phyllodicola Delamare Deboutteville & Laubier, 1961

Syn: *Phyllocola* Delamare Deboutteville & Laubier, 1960 (preoccupied) Non *Phyllocola* Gistl, 1848 (Coleoptera)

**Diagnosis**. Adult female body (ectosoma) highly transformed, unsegmented, attached via short broad stalk to endosoma embedded within host. Ectosoma ovoid, about 400 to 900 µm in length (Fig. 9A), varying with reproductive state (cf. Fig. 13A–C). Anus lacking. Paired genital apertures present, located on ventral surface anterior to mid-level; each aperture with two strong tooth-like elements (Fig. 11B). Paired copulatory pores (arrowed in Fig. 11B) located on ventral surface adjacent to genital apertures. Egg strings elongate, with large eggs attached to central axial filament (cf. Fig. 13A). Antennule (Fig. 9C) located dorsal to stalk, unsegmented, tapering towards tip, armed with array of stout setal elements along anterior and apical margins. Antenna (Fig. 11D) with broad basal segment bearing, posteriorly, robust, indistinctly 2-segmented endopod armed with 4 apical claws; basal segment produced anteriorly into lobe ornamented with minutely spinulose lamellae. Maxilliped (Fig. 11E) subchelate, comprising robust basal segment plus subchela consisting of long proximal segment and compound apical segment armed with 3 strong claws on distal margin. Stalk originating on underside of ectosoma in oral region. Endosoma taking form of two elongate rootlets penetrating body cavity of host, with several short digitiform processes originating around base of primary rootlets. Male unknown. Nauplius lecithotrophic, with nauplius eye.

Type species: *Phyllodicola petiti* (Delamare Deboutteville & Laubier, 1960)

**Remarks**. The development of the ectosoma can be reconstructed by reference to Laubier (1961): in the very early stage a vestigial abdominal process is still visible (Laubier 1961: Fig. 3b) but this is absorbed during subsequent development so the mature adult female has an ovoid ectosoma lacking any trace of a defined abdomen.

We interpret the uniramous antenna slightly differently from Laubier (1961). We interpret the ramus as ornamented with claws that are flattened and very broad at the base so they are rather lamellate in form. The compound apical segment of the maxilliped shows bands of thickening (Fig. 11E) which appear to correspond to at least two incompletely expressed segments. It is this segmentation pattern that provides the evidence supporting the interpretation of these limbs as maxillipeds rather than maxillae, since the maxilla exhibits a maximum of two expressed segments in all members of the poecilostome lineage within the order Cyclopoida (Huys & Boxshall 1991).

# Phyllodicola petiti (Delamare Deboutteville & Laubier, 1960)

Syn: Phyllocola petiti Delamare Deboutteville & Laubier, 1960

**Norwegian material examined**: 1 $\bigcirc$  from *Eumida ockelmanni* Eibye-Jacobsen, 1987, Veslefrikk, Stn 5-4 (60.7825°N, 02.901°E), depth 175 m, 16 May 1998; collected by A. Sikorski; NHMUK Reg. No. 2015.3013. 1 $\bigcirc$  from *E. ockelmanni*, Kakshauger, Stn 17-4 (59.7334°N, 02.35689°E), depth ~100 m, 12 June 2000; collected by A. Sikorski; NHMUK Reg. No. 2015.3014. 1 $\bigcirc$  from *E. ockelmanni*, Oseberg Øst, Stn 2-4 (60.7032°N, 01.9406°E), depth 155 m, 25 May 2004; collected by A. Sikorski; NHMUK Reg. No. 2015.3015. 1 $\bigcirc$  from *E. ockelmanni*, Oseberg J, Stn 2-5 (60.3571°N, 02.9408°E), depth 100 m, 29 May 2004; collected by A. Sikorski; NHMUK Reg. No. 2015.3016. 1 $\bigcirc$  from *E. ockelmanni*, Gullfaks Satelitter, Stn F/G1-1 (61.0951°N, 02.277367°E), depth 134 m, 02 June 2005; collected by A. Sikorski; NHMUK Reg. No. 2015.3017. 1 $\bigcirc$  from *E. ockelmanni*, 7982 Gaukvaerøy, Stn Ga 3-2 (68.61698°N, 14.35522°E), depth 38 m, 02 December 2015; collected by A. Sikorski; NHMUK Reg. No. 2016.551. 1 $\bigcirc$  from *Eumida sanguinea* (Örsted, 1843), 7262 Brettingen C, Stn 2 (63.35525°N, 08.238833°E), depth 91 m, 30 September 2014; collected by A. Sikorski; NHMUK Reg. No. 2017.467.

**British material examined:** 1 mature  $\bigcirc$  and 1 juvenile  $\bigcirc$  from *E. sanguinea*, Irvine Bay, SEPA Stn R2 (55° 33.88'N, 04° 41.65'W), depth 13 m, 29 July 1994. 2 ovigerous  $\bigcirc \bigcirc$ , 1 juvenile  $\bigcirc$  from *E.?ockelmanni*, Vidlin Voe, Shetland Mainland, Stn Vid 0A, depth unknown, 25 April 2000; collected by P. R. Garwood. 1 juvenile  $\bigcirc$  from *E.?ockelmanni*, North Sandwick, Yell, Shetland, depth unknown, 24 April 2000; collected by P. R. Garwood. 2 juvenile  $\bigcirc \bigcirc$  from *E. ockelmanni* (2 mm body length) Vidlin Voe, Shetland Mainland, Stn 50B, depth unknown, 25 April 2000; collected by P. R. Garwood. 2 mature  $\bigcirc \bigcirc , 2$  juvenile  $\bigcirc \bigcirc \bigcirc$  from *E. ockelmanni* (1.75 mm body length),



**FIGURE 11**. *Phyllodicola petiti* (Delamare Deboutteville & Laubier, 1960), female. A, ectosoma and proximal part of endosoma; B, genital apertures and copulatory pores (arrowed); ventral; C, antennule; D, antenna; E, maxilliped. Scale bars: A, 200 µm, B, 100 µm, C–E, 25 µm.

Basta Ness, Yell, Shetland, depth unknown, 2000; collected by P. R. Garwood. 1 juvenile  $\bigcirc$  from *E. ockelmanni*, North Havra, Shetland, depth unknown, 2000; collected by P. R. Garwood. 2 ovigerous  $\bigcirc \bigcirc \bigcirc$  from *E. ockelmanni*, Collafirth, Shetland Mainland, depth unknown, 30 July 2008; collected by P. R. Garwood. 1 ovigerous  $\bigcirc \bigcirc$  from *E.* 

*ockelmanni*, Papa, The Deeps, Shetland, depth unknown, 2000; collected by P. R. Garwood. 1 ovigerous  $\bigcirc$ , 6 immature  $\bigcirc \bigcirc$  from four *E. ockelmanni*, Shetland, depth unknown; collected by P. R. Garwood. 1  $\bigcirc$  from *E. ockelmanni*, Foreholm, The Deeps, Shetland, depth unknown, 2002; collected by P. R. Garwood. NHMUK Reg. Nos 2010.1064-1068. 1 ovigerous  $\bigcirc$  from *E. sanguinea*, Cloch Point, Firth of Clyde, SEPA Stn CMT7 (55° 56.85'N, 04° 53.65'W), depth 80 m, 14 April 2003; collected by M. O'Reilly. 1 mature  $\bigcirc$ , 1 juvenile  $\bigcirc$  from Phyllodocidae sp. indet., Eastern English Channel, no collection data. 2 juvenile  $\bigcirc$  from *E. ockelmanni*, Orkney, Veantrow, SEPA Stn 200mS (59° 04.401'N, 02° 52.178'W), depth 10 m, 14 June 2016. NHMUK Reg. Nos 2018.139-142.

# Differential diagnosis. As for genus.

**Remarks**. The new material confirms the majority of the observations made by Laubier (1961). None of the females collected from *E. ockelmanni* or *E. sanguinea* in Norwegian waters was ovigerous. The mouthparts (Fig. 11D, E) were dissected on an adult female with an ectosoma length of 373  $\mu$ m. The antennule (Fig. 11C) is a tapering unsegmented lobe bearing 14 stout setal elements, which is within the range of setal numbers given by Laubier (1961). Slight differences in reported setation counts probably reflect the difficulty in observing these small structures.

The type host was *Eulalia pusilla* Örsted, 1843 collected at depths ranging from 25 to 280 m (Laubier 1961). O'Reilly (2000) reported *P. petiti* from Scottish waters on three hosts, *Phyllodoce rosea* (McIntosh, 1877), *Eumida bahusiensis* Bergström, 1914, and *E. sanguinea*. The common host reported here, *E. ockelmanni*, is a new host record for this parasite and the depth range for parasitised hosts was 10 to 175 m. All of these hosts belong to the family Phyllodocidae, as does *Eteone* Savigny, 1818, the host of the genus *Cyclorhiza*.

#### Genus Cyclorhiza Heegaard, 1942

**Diagnosis**. Adult female highly transformed; ectosoma globular to cylindrical (Fig. 13A–E), with rudimentary urosomal region located antero- or mid-ventrally in young females of one species. Ectosoma attached via short stalk penetrating body wall of host. Stalk broad, connecting to endosoma formed by pair of slender buccal rootlets lying within body cavity of host. Endosoma sometimes with additional irregular processes at base of primary rootlets. Genital apertures paired, located anteroventrally on ectosoma (Fig. 13A, C, D). Antennule unsegmented, tapering, setose (Fig. 13G). Antenna uniramous, with broad basal segment expanded into concave process, plus 2-segmented endopod bearing claws at apex (Fig. 13H). Mandible, maxillule and maxilla all apparently absent in adult. Maxilliped well developed; subchelate comprising large partially subdivided proximal segment and distal subchela bearing 3 strong claws distally (Fig. 13I). Egg sacs multiseriate (Fig. 12, 13B), or extruded as elongate egg strings which break down, so mature eggs attached separately to axial filament (Fig. 13A). Male unknown. Nauplius lecithotrophic, with typical nauplius eye.

Type species: Cyclorhiza eteonicola Heegaard, 1942, by original monotypy.

**Remarks**. *Cyclorhiza* comprises two species: *C. eteonicola* described from *Eteone longa* (Fabricius, 1780) taken near Trondheim in southwestern Norway (Heegaard 1942), and *C. megalova* Gotto & Leahy, 1988 described from the same host species taken in Galway Bay in western Ireland (Gotto & Leahy 1988). The genus was originally placed in the Herpyllobiidae by Heegaard (1942) but was subsequently transferred to the Phyllodicolidae by Lützen (1964a).

# Cyclorhiza eteonicola Heegaard, 1942

**Material examined**: 1 ovigerous  $\bigcirc$  from *Eteone spetsbergensis* Malmgren, 1865, 3697 Svalbard, Adventfjorden, Stn 5-4 (78° 13'00"N, 15° 13'00"E), depth 30-60 m, 08 September 2011; collected by A. Sikorski; NHMUK Reg. No. 2016.520.

**Differential diagnosis.** Adult female body comprising ectosoma connected to endosoma via short stalk. Ectosoma of mature female 2.1 times longer than maximum width (length 0.93 mm, maximum width 0.44 mm); tapering posteriorly. Ectosoma bearing antennules, antennae and maxillipeds typical for genus; lacking any vestige of trunk limbs and caudal rami. Anus lacking. Genital apertures paired, located anteriorly on underside of

ectosoma. Egg sacs 4.55 mm long: egg arrangement multiseriate with about 5 longitudinal rows visible in any view (Fig. 12); eggs spherical, mean diameter 92  $\mu$ m (range 84 to 104  $\mu$ m). Stalk short and broad, connecting to endosoma within host. Endosoma comprising 2 elongate rootlets penetrating body cavity of host.

**Remarks**. Heegaard (1942) based his original description on two females found on *Eteone longa* collected in sand on an island beach outside Trondheim fjord (western Norway). It was subsequently reported from the east coast of North America by Lützen (1964b) on *E. longa*. The female recorded here was collected from *Eteone spetsbergensis*, a new host, and it was attached in the mid-body region of its host (Fig. 10). *Cyclorhiza eteonicola* was reported from UK waters by O'Reilly & Geddes (2000), who found 5 non-ovigerous females on *E. longa* near Holy Island, off the coast of Northumberland. However, O'Reilly (2000) subsequently concluded that this material could equally be attributed to *C. megalova* since egg size is diagnostic and these specimens were non-ovigerous.



FIGURE 12. Cyclorhiza eteonicola Heegaard, 1942. Micro-CT rendering of ovigerous female attached to host, Eteone spetsbergensis. Scale bar: 2 mm.

# Cyclorhiza megalova Gotto & Leahy, 1988

**Norwegian material examined**:  $49 \bigcirc \bigcirc$  from 34 specimens of *Eteone* cf. *longa/flava*, 4909 Helgeland, Havbruk, Stn 1 (69.9202°N, 12.24907°E), depth 115 m, 12 November 2007; collected by A. Sikorski.  $3 \bigcirc \bigcirc$  from 2 specimens

of *Eteone* cf. *longa/flava*, Sandnessjøen, Stn LÅ1 (66.2301°N, 12.32355°E), depth 48 m, 03 January 2007; collected by A. Sikorski. 1 $\bigcirc$  from *Eteone* cf. *longa*, 5769 Brattholmen, Stn S2-B (65.9106°N, 12.22213°E), depth 115 m, 18 January 2001; collected by A. Sikorski. 1 $\bigcirc$  from *Eteone* cf. *longa/flava*, 5161 Korsfjord, Stn D5 (70.2347°N, 23.35317°E), depth 131 m, 27 September 2010; collected by A. Sikorski. 1 $\bigcirc$  from *Eteone* cf. *longa/flava*, 5161 Korsfjord, Stn D5 (70.2347°N, 23.35317°E), depth 131 m, 27 September 2010; collected by A. Sikorski. 1 $\bigcirc$  from *Eteone* cf. *longa/flava*, Huldra, Stn 6-1 (60.853°N, 02.640619°E), depth 123 m; 05 June 1999; collected by A. Sikorski. 1 $\bigcirc$  from *Eteone* cf. *longa/flava*, Huldra, Stn 13-1 (60.8572°N, 02.646196°E), depth 123 m; 05 June 1999; collected by A. Sikorski. 6 $\bigcirc$   $\bigcirc$  *Eteone* cf. *longa/flava*, 7734 Bjørnsvik 2015, Stn 3B (67.53188°N, 15.38787°E), depth 247 m, 03 June 2015; collected by A. Sikorski. 1 $\bigcirc$  *Eteone* cf. *longa/flava*, 8190 Hammer ASC, Stn C5-2 (67.96118°N, 15.16742°E), depth 68 m, 31 March 2016; collected by A. Sikorski. NHMUK Reg. Nos 2016.527-536.

**British material examined**: 1 mature  $\bigcirc$  from *E. longa*, Shetland Mainland, Vidlin Voe, Stn 50B, depth unknown, 25 April 2000; collected by P. R. Garwood. 2 mature  $\bigcirc \bigcirc$ , 5 immature  $\bigcirc \bigcirc \bigcirc$  from 4 specimens of *Eteone longa* (Fabricius, 1780), North Sea, Dockhead A; depth unknown, 2006; collected by P. R. Garwood. 1 mature  $\bigcirc$  from *E. longa*, (Unico. 43242), Survey MARCOD08, Codling Bank, Stn 16a, 18 September 2008, collected David Hall. 1 ovigerous  $\bigcirc$  from *E. longa*, Irish Sea, Cork, depth unknown, 26 October 2011; collected by P. R. Garwood. 4 ovigerous  $\bigcirc \bigcirc \bigcirc$ , 1 mature  $\bigcirc$ , from 4 specimens of *E. longa*, Cairn Ryan, Loch Ryan, 13 March 2012, collected by David Hall. 1 ovigerous  $\bigcirc, 3$  mature  $\bigcirc \bigcirc, 2$  immature  $\bigcirc \bigcirc \bigcirc$  from 5 specimens of *E. longa*, Loch Ryan, SEPA Stn West of Drummuckloch, Cairn Ryan (54° 57.216'N, 05° 01.299'W), depth 10 m, 11 July 2013; collected by Jeni Boyle. 3 mature  $\bigcirc, 3$  juvenile  $\bigcirc$  from single *E. longa*, Orkney, Veantrow, SEPA Stn 200mS (59° 04.401'N, 02° 52.178'W), depth 10 m, 14 June 2016. 2 mature  $\bigcirc \bigcirc \bigcirc \bigcirc \odot$  on *E. longa*, Shetland, Hascosay Sound, Bow of Hascosay Fish Farm, SEPA Stn 100mN (60° 36.80'N, 01° 00.34'W), depth 11 m, found by Jeni Boyle, 03 June 2017. 1 ovigerous  $\bigcirc$  on *E. longa*, Shetland Mainland, Setterness West Fish Farm, SEPA Stn 100mNW (60° 25.26'N, 01° 00.09'W), depth 55 m, found by Jeni Boyle, 13 June 2017. NHMUK Reg. Nos 2018.143-152.

**Differential diagnosis**. Adult female body comprising elongate ectosoma connected to endosoma via short stalk. Ectosoma of mature female with mean length 1.22 mm, range 0.84 mm to 1.65 mm (based on 12 ovigerous specimens), and mean maximum width of 0.31 mm, range 0.23 to 0.40 mm. Ectosoma variable in shape, typically tapering posteriorly (Fig. 13A, B), but blunt ended in developing females (Fig. 13D) and in adult females prior to oviposition (Fig. 13C). Ectosoma bearing antennules, antennae and maxillipeds (Figs. 13G-I) typical for genus; lacking any vestige of trunk limbs and caudal rami. Anus lacking. Genital apertures paired, located anteriorly on underside of ectosoma (Fig. 13F). Egg sacs elongate, up to 4.83 mm long (in female of body length 1.38 mm), egg arrangement typically multiseriate with 2 or 3 irregular longitudinal rows visible in any view (Fig. 13B). Eggs ovoid: mean dimensions 122  $\mu$ m (long axis) by 93  $\mu$ m (short axis). Stalk short and broad, connecting to endosoma within host. Endosoma comprising two elongate rootlets, penetrating body cavity of host.

**Remarks**. We agree with the interpretation of Gotto & Leahy (1988) that the form of the endosoma described for this species by Heegaard (1942) was inaccurate due to damage. The endosoma comprises two elongate rootlets. More than 20 ovigerous females were examined and all but one possessed multiseriate egg sacs up to 4.83 mm in length, although the egg sacs were often broken. The single exception was a female of ectosoma length 0.96 mm which carried an egg sac in the form of an axial filament with eggs attached along its length (Fig. 13A), described as a "bunch of grapes" by Gotto & Leahy (1988). A similar form of egg sacs was illustrated for *Phyllodicola petiti* by Delamare Deboutteville & Laubier (1960). These eggs were ovoid and of the same dimensions as those measured in multiseriate sacs (i.e. about 122 by 93  $\mu$ m). The average of these measurements (108  $\mu$ m) corresponds closely to the single dimension for egg size (110  $\mu$ m) given by Gotto & Leahy (1988) and this character was used by Gotto (1993) to distinguish between the two congeners, since the eggs are markedly smaller in *C. eteonicola* (92  $\mu$ m). In addition, the multiseriate egg sacs of *C. megalova* typically display 2 or 3 longitudinal rows of eggs within the sac (Fig. 13B), whereas in *C. eteonicola* the egg sacs display about 5 longitudinal rows (Fig. 12). There were no significant differences in limb structure between *C. megalova* and *C. eteonicola*.

Some of the hosts are reported here as *Eteone* cf. *longa/flava* as the polychaete material from Norwegian waters was not assigned to species level. The depth range of this parasite in Norwegian waters is 48 to 247 m. O'Reilly (2000) recorded *C. megalova* on *E. longa* caught in Orkney, Loch Craignish (Argyll) and the Firth of Clyde in Scotland, and from the same host in the Irish Sea.



**FIGURE 13**. *Cyclorhiza megalova* Gotto & Leahy, 1988, female. A, spent adult female with single egg string attached, ventral view showing egg string comprising central axis and large developing eggs plus empty egg membranes (arrowed); B, adult female showing length of intact egg sac relative to ectosoma length; C, adult female with ectosoma full of developing eggs; D, developing ectosoma; E, early stage female, lateral view showing paired limbs, genital apertures and finely striated dorsal surface integument; F, detail of developing female anterior end, showing spinules (arrowed) located lateral and medial to genital aperture; G, antennule; H, antenna; I, maxilliped. Scale bars A, C–D, 200 μm, B, 1 mm, E, 50 μm, F, 100 μm, G–I, 25 μm.

#### Family Saccopsidae Lützen, 1964

This family of highly transformed copepods was established by Lützen (1964b) to accommodate *Saccopsis* Levinsen, 1878 but Bresciani & Lützen (1975) later recognised that *Saccopsis* was a junior synonym of *Melinnacheres* M. Sars, 1870. Subsequently Boxshall (1977) relegated *Oestrella* M'Intosh, 1885 to synonymy with *Melinnacheres*. Boxshall & Halsey (2004) provided a key to the four valid species of *Melinnacheres*. Prior to the present study the family comprised only the single genus, although a possible relationship with the genus inquirendum *Flabellicola* Gravier, 1918, found on *Flabelligera diplochaitus* (Otto, 1820) in the Mediterranean (Gravier 1918), was noted by Boxshall & Halsey (2004).

# Subfamily Saccopsinae Lützen, 1964

This subfamily is established here to accommodate the typical saccopsids characterized by the form of the adult female antennae and maxillae. In the Saccopsinae the antennae are located on the ventral surface of the oral region, anterior to the stalk which connects the large ectosoma and the small bulla-like endosoma. They are 2-segmented and the apical segment carries paired distal pads. The maxillae each comprise a robust basal segment and a terminal segment typically also bearing paired adhesion pads. This subfamily comprises *Melinnacheres* plus two new genera described below, *Trichobranchicola* gen. nov. and *Lanassicola* gen. nov. Another two new genera, *Euchonicola* gen. nov. and *Euchonicoloides* gen. nov., are placed in a new subfamily, Euchonicolinae subfam. nov., established below.

#### Genus Melinnacheres M. Sars, 1870

Syn: *Saccopsis* Levinsen, 1878 *Oestrella* M'Intosh, 1885

**Diagnosis**. Adult female typically with unsegmented ovoid to conical body (ectosoma), attached to host via short stalk located anteriorly on ventral surface, leading to short bulla (endosoma) inserted in host. Ectosoma lacking defined cephalothorax but retaining paired antennules, antennae and maxillae located around base of stalk originating in oral region. Trunk often with paired surface depressions or internal cuticular sutures representing traces of segmental organization; lacking any vestiges of post-cephalic limbs. Genital apertures paired, carried on conspicuous swellings located on or near posterior margin. Paired cement glands curved, well developed and visible through body wall. Median anal prominence with anal slit present or absent. Egg sacs paired, multiseriate.

Adult male ovoid, indistinctly divided into anterior cephalothorax and posterior trunk. Cephalothorax bearing paired antennules frontally plus antennae and maxillae located around oral region. Oral region with funnel-like chitinous framework enclosing paired lobate structures possibly representing mandibles. Trunk lacking vestiges of limbs. Caudal rami absent. Antennules indistinctly segmented, setose. Antennae 2-segmented with paired apical pads. Maxillae with robust proximal segment and broad distal segment bearing paired adhesion pads.

Type species: Melinnacheres ergasiloides M. Sars, 1870, by original monotypy.

**Remarks**. *Melinnacheres* is a distinctive genus characterised by its undifferentiated ectosoma bearing three pairs of cephalic appendages located in the oral region around the base of the stalk. The small bulla-like endosoma is also distinctive, differing markedly from the large endosoma of the Bradophilidae, Herpyllobiidae, and Phyllodicolidae. The characteristics of the dwarf adult males were first elucidated in detail by Bresciani & Lützen (1975). Species of this genus have been reported from ampharetid and terebellid hosts.

# Melinnacheres ergasiloides M. Sars, 1870

**Material examined**: 3 ovigerous  $\bigcirc \bigcirc$  from *Melinna elisabethae* McIntosh, 1914, Resi Stagnes, Stn 5-2 (68° 48.459'N, 16° 36.753'E), depth 74 m, 28 May 2006; collected by A. Sikorski; NHMUK Reg. Nos 2015.3004-3006. 1 ovigerous  $\bigcirc$  from *M. elisabethae*, Argus Miljø, Stn Ø2-2 (67° 14.692''N, 15° 23.094'E), depth 145 m, 2009;

collected by A. Sikorski; NHMUK Reg. No. 2015.3007. 1 ovigerous  $\bigcirc$  from *M. elisabethae*, Norvarg, Stn 1-4 (72.88696°'N, 25.79947°E), depth 371 m, 29 May 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.3008.

**Differential diagnosis.** Body of adult female ovoid in outline (Fig. 14A, B), dorsoventrally flattened; mean body length 0.99 mm (range 0.93 to 1.08 mm, based on 5 ovigerous specimens); body from 1.38 to 1.94 times longer than wide (mean = 1.6 times) according to state of contraction (cf. Fig. 14A, B). Ventral longitudinal trunk muscles visible through ventral body wall and transverse internal sutures also visible, marking planes of former inter-segmental boundaries and providing attachment sites for longitudinal trunk muscles (Fig. 14B). Paired genital apertures carried on conspicuous genital swellings located ventrally near posterior margin. Small anal prominence with median anal slit, present dorsally above mid-posterior margin (Fig. 14C). Female attached to host via short stalk located anteriorly on ventral surface, leading to short bulla (endosoma) inserted in host. Paired antennules, antennae and maxillae present around base of stalk (Fig. 14A). Antennules short, tapering distally, indistinctly subdivided into broader basal segment and tapering distal segment armed with apical seta. Antennae located anterior to stalk, orientated transversely with apex directed towards midline: 2-segmented, basal segment unarmed, apical segment with paired distal adhesion pads. Maxillae located posterior to stalk; comprising robust basal segment with inner distal corner produced into spinous process; terminal segment bearing 2 adhesion pads. Cement glands short, extending only 30% of length of trunk, lying within zone derived from fourth pedigerous somite (Fig. 14B). Egg sacs weakly curved, irregularly biseriate (Fig. 14D).

Adult male body ovoid, indistinctly divided into anterior cephalothorax and tapering posterior trunk (Fig. 14E, F); body length about 155 µm, maximum width about 100 µm, at anterior part of trunk. Cephalothoracic region bearing paired antennules, antennae and maxillae surrounding oral region. Trunk lacking defined limbs. Ventral surface of trunk ornamented with dense covering of fine spinules (Fig. 14F). Antennules elongate, tapering towards tip, indistinctly segmented; armed with 3 setae along anterior margin and 3 setal elements around tip (Fig. 14E, F). Antennae 2-segmented (Fig. 14F); basal segment unarmed, apical segment with 2 rounded apical pads. Paired labral processes present either side of ventral midline, just anterior to chitinous oral framework. Oral region defined by sub-rectangular framework of chitinous thickenings enclosing paired, medially-directed, rounded spinose pads (Fig. 14F), interpreted as mandibles by Bresciani & Lützen (1975). Maxilla (Fig. 12F) comprising robust basal segment with inner distal corner produced into blunt-tipped spinous process; distal segment bearing 2 adhesion pads ornamented with dense covering of fine spinules.

**Remarks**. *Melinnacheres ergasiloides* was originally reported from the ampharetid worm *Melinna cristata* (M. Sars, 1870) caught in Oslofjord in southern Norway (M. Sars 1870). Sars described and illustrated the external morphology of both sexes in detail. Over a century later, Bresciani & Lützen (1975) redescribed both sexes on the basis of new material collected from the same host, *M. cristata*, caught off the western Swedish coast in the Skagerrak, and they also provided preliminary observations on the internal anatomy of the female.

The material examined here all comes from *Melinna elisabethae* caught off the coast of northern Norway in Arctic latitudes from  $67^{\circ}$  to nearly  $73^{\circ}$  N and at depths of 74 to 371 m. This is a new host record for *M. ergasiloides*. The new material conforms closely to *M. ergasiloides* as redescribed by Bresciani & Lützen (1975) but there are some differences: Bresciani & Lützen (1975) showed the antennules of the female as elongate and indistinctly 6-segmented, quite similar to that of the male. The antennules of females from *M. elisabethae* examined here are much shorter and indistinctly 2-segmented. These reduced limbs are difficult to observe in the large females so we tentatively interpret this difference as due to the state of preservation of the material.

We also differ from Bresciani & Lützen (1975) in our interpretation of the oral area of the adult male, in particular, in the form of the mandibles. The oral region of the male includes a pair of small processes, referred to here as labral processes, which were clearly visible in Bresciani & Lützen's illustration (1975, fig. 6) and were referred to as sinuous structures continuous with the anterior margin of the buccal armature. Bresciani & Lützen (1975) described the mandibles as unsegmented and terminating in a "broad comb and blunt anterior-directed projection". We were unable to observe a comb, but the surface of the rounded basal part was densely ornamented with spinules in our material. The identification of this paired structure as mandibles is based on inferences made by Bresciani & Lützen (1975), who examined the transitional developmental stage, the copepodid.

The female in figure 14A carries three conical structures attached to the ventral body surface in the genital region (arrowed in Figure). Each has a circular base which adheres to the body surface of the female and a tapering distal part that may be slightly twisted. We identify these structures as spermatophores and, after studying the male of *Lanassicola arcticus* gen. et sp. nov. described below, we propose a novel method of deposition for spermatophores in male saccopsids (see below).



**FIGURE 14**. *Melinnacheres ergasiloides* M. Sars, 1870. A, ovigerous female detached from host, ventral view showing 3 attached spermatophores (arrowed); B, another female with 2 males attached, ventral view showing longitudinal trunk musculature of female; C, posterior margin of trunk showing paired genital apertures and anal slit on median prominence; D, egg sac; E, adult male, dorsal view; F, same, ventral view showing paired appendages and surface ornamentation. Scale bars: A–B, D, 0.5 mm, C, 250 µm, E–F, 100 µm.

The female parasites on *M. elisabethae* were all attached laterally in the mid-body region around the junction between thorax and abdomen of the worm, in the vicinity of the 18th setiger, as illustrated by Bresciani & Lützen (1975: Fig. 1) for their material of *M. ergasiloides* from *Melinna cristata*.

# Melinnacheres steenstrupi (Bresciani & Lützen, 1961)

#### Syn: Saccopsis steenstrupi Bresciani & Lützen, 1961

Norwegian material examined: 19 from *Terebellides stroemi*-complex, Ba-1992, Slope between Spitsbergen Bank and Hopen Trough, Stn 14-3 (75° 22.0'N, 26° 37.0'E), depth 189 m, 09 August 1992; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Glitne, Stn 6-5 (58.71169°N, 01.675149°E), depth ≈105 m, 30 May 2000; collected by A. Sikorski. 1♀ from T. stroemi-complex, R/V "Jan Mayen", Hinlopen, Stn 1137-1 (79.67333°N, 18.62767°E), depth 267 m, 21 September 2001; collected by A. Sikorski. 1♀ from T. stroemi-complex, Alfa Nord, Stn A-1, 0-3 (58° 29.946'N, 01° 43.422'E), depth 108 m, 04 – 11 September 2003; collected by A. Sikorski. 1♀ from T. stroemi-complex, SVAN, Stn ALF 3 (58.5059°N, 01.7591°E), depth 108 m, 20 April 2004; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Oseberg Øst, Stn 16-2 (60.6746°N, 02.986°E), depth 157 m, 24 May 2004; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Oseberg Øst, Stn 18-5 (60.7127°N, 02.9082°E), depth 152 m, 25 May 2004; collected by A. Sikorski.  $4 \bigcirc \bigcirc$  from 3 specimens of *T. stroemi*-complex, Troll B, Stn 10-1 (60.7112°N, 03.5105°E), depth 314 m, 02 June 2004; collected by A. Sikorski. 1 $\bigcirc$  from T. stroemi-complex, Barents Sea, Hopen Bank Stn 12-5 (75° 55.1'N, 25° 19.2'E), depth 111 m, 24 May 2005; collected by A. Sikorski. 1♀ juvenile from T. stroemi-complex, Nucula, Stn 2-3 (71.55047°N, 25.23236°E), depth 292 m, 05 September 2006; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  juveniles from *Terebellides stroemi*-complex, Nessar, Hopen Bank slope Stn G-14 (75° 21.94'N, 26° 37.12'E), depth 191 m, 16 August 2007; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  from 2 specimens of T. stroemi-complex, Nessar, Stn G-12 (75° 55.12N, 25° 20.88'E), depth 111 m, 29 April 2008; collected by A. Sikorski. 2  $\bigcirc$  juveniles from *T. stroemi*-complex, Kristin, Stn Q5-5 (64.85565°N, 06.451107°E), depth 330 m, 06 June 2009; collected by A. Sikorski. 6  $\bigcirc$  from 2 specimens of *T. stroemi*-complex, Codfarmers, Mørkvedbukta, Stn Dyp1-2 (67° 16.591'N, 14° 33.314'E), depth 32 m, 15 July 2009; collected by A. Sikorski. 1♀ from *T. stroemi*complex, Mareano 2010110, Stn 531, sample 389 (70° 42.0081'N, 18° 33.3673'E), depth 372 m, 31 July 2010; collected by A. Sikorski. 1♀ from T. stroemi-complex, Niva 2014, Stn 525 - G, sample B05-IIIE (58.3252°N, 08.6295°E), depth 52 m, 02 March 2013; collected by A. Sikorski. 1♀ from T. stroemi-complex, 7886 Daljorda, Stn Da 3-2 (68.68988°N, 14.96113°E), depth 181 m, 24 September 2015; collected by A. Sikorski. NHMUK Reg. Nos 2016.553-562. 5♀♀ from 2 specimens of *Terebellides atlantis* Williams, 1984, 5796 Yttergryta 2012, Stn YTG7-4 (65.10969°N, 07.512037°E), depth 302 m, 29 May 2012; collected by A. Sikorski. 1♀ from *T. atlantis*, 5463 Stjernsund, Stn 12-3 (70.27983°N, 22.4015°E), depth 402 m, 15 August 2012; collected by A. Sikorski; NHMUK Reg. Nos 2016.521-526.

**British materal examined**: 1 ovigerous  $\bigcirc$ , 1 mature  $\bigcirc$  from gill of *T. stroemi*, Shetland BGI, depth unknown, 2002; collected by P. R. Garwood. 1 mature  $\bigcirc$  from gill of *T. stroemi*, Shetland BGIN S5OA, depth unknown, 2003; collected by P. R. Garwood. 5 ovigerous  $\bigcirc \bigcirc \bigcirc$  from single specimen of *T. stroemi*, Shetland, Flotta Stn N50B, depth unknown, 2003; collected by P. R. Garwood; NHMUK Reg. Nos 2017.487-490. 7 mature and juvenile  $\bigcirc \bigcirc$  on gills of *T. stroemi*, Skye, Loch Greshornish, depth unknown, 07 July 2004; collected by P. R. Garwood. 2 ovigerous  $\bigcirc \bigcirc \bigcirc$  from single *T. stroemi*, Cole Deep, depth unknown, 2004; collected by P. R. Garwood. 1 ovigerous  $\bigcirc$  from gill of *T. stroemi*, Belfast Lough, North Channel, EHS Stn CON/Muck Isle C, (54° 50.5101'N, 05° 42.8499'W), depth 16 m, collected 14 March 2013 by Tim Mackie. NHMUK Reg. Nos 2018.153-162.

**Differential diagnosis**. Adult female body ovoid (Fig. 15A) and lacking externally expressed segmentation: mean ectosoma length 1.18 mm, with range of 0.57 to 1.94 mm (based on 10 ovigerous specimens), mean width 0.92 mm (range 0.55 to 1.65 mm), mean depth 0.77 mm (range 0.35 to 1.61 mm). Paired genital openings carried on prominent swelling located close together (Fig. 15A) on posterior margin of ectosoma. No anal opening present. Paired cement glands conspicuous, located in posterior part of ectosoma and extending anteriorly up to 40% of ectosoma length (Fig. 15A–C). Egg sacs multiseriate (Fig. 15D); typically curved and from 1.4 to 2.5 times longer than ectosoma; mean length 1.69 mm (range 0.88 to 3.87 mm).



**FIGURE 15**. *Melinnacheres steenstrupi* Bresciani & Lützen, 1961. A, ovigerous female, dorsal; B, same, ventral; C, same, lateral; D, detached egg sac. *Melinnacheres terebellidis* Levinsen, 1878. E, ovigerous female, dorsal; F, same ventral; G, detached egg sac. All scale bars 1 mm.

**Remarks**. The original description of *M. steenstrupi* included data on the external morphology and internal anatomy of the female, based on serial sections, as well as descriptions of the adult male and a late copepodid stage (Bresciani & Lützen 1961). Bresciani & Lützen (1961) distinguished *M. steenstrupi* from its congener *M. terebellidis*, which occurs on what was regarded as the same host at that time (under the name *Terebellides stroemi*) by reference to female body size which was up to 1.8 mm in the former compared with up to 4.0 mm in the latter. Based in part on observations made on live material, Bresciani & Lützen (1961) also stated that *M. steenstrupi* has an ovoid body shape in contrast to the more oblong, conical body of *M. terebellidis*, and that the paired swellings bearing the female gonopores are larger and positioned closer together in the former than in the latter.

We found that the body shape and form of the genital swellings varies a little according to the state of contraction of the fixed specimens but the basic shape of *M. steenstrupi* is more globular and can be readily differentiated from the tapering and more flattened *M. terebellidis*. Our material of *M. steenstrupi*, with its mean ectosoma length of 1.18 mm for ovigerous females (range 0.57 to 1.94 mm), is smaller than that examined by O'Reilly (2016) who reported a mean length of 1.6 mm (range 1.24 to 1.88 mm). O'Reilly's material of *M. steenstrupi* came from the western Scotland, but included some specimens from the southern North Sea, the Celtic Sea and from Kosterfjord (Sweden).

Previous reports of *M. steenstrupi* are largely from *Terebellides stroemi*, however this is now recognised to be a species complex, so the majority of the hosts examined during this study were identified only as *T. stroemi*-complex. In addition, we report here *M. steenstrupi* on *T. atlantis* for the first time.

#### Melinnacheres terebellidis (Levinsen, 1878)

#### Syn: Saccopsis terebellidis Levinsen, 1878

Norwegian material examined:  $1^{\circ}$  from *Terebellides stroemi*-complex, TOGI, Stn 10-4 (60.57633°N, 03.65566°E), depth 304 m, 10 May 1998; collected by A. Sikorski. 19 from T. stroemi-complex, Sygna, Stn 5-2 (61.4645°N, 1.98727°E), depth 296 m, 11 June 1999; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  from *T. stroemi*-complex, Statfjord A, Stn 9-5 (61.26239°N, 01.839069°E), depth 147 m, 15 June 1999; collected by A. Sikorski. 1♀ from *T*. stroemi-complex, Gullfaks Satelitter, Stn GFK 3-4 (61.12791°N, 02.023441°E), depth 138 m, 18 June 1999; collected by A. Sikorski. 1♀ from *Terebellides* sp., Gullfaks Satelitter, Stn GFK 2-5 (61.0518°N, 02.078563°E), depth 134 m, 21 June 1999; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Gullfaks Satelitter, Stn GFH1-3 (61.05359°N, 02.075616°E), depth 134 m, 21 June 1999; collected by A. Sikorski.  $1^{\circ}$  from *Terebellides* sp., Vigdis, Stn 3-2 (61.39485°N, 02.072259°E), depth 278 m, 31 May 1999; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  from T. stroemi-complex, Oseberg East, Stn 3-4 (60.70634°N, 02.946468°E), depth 164 m, 23 May 2000; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Oseberg East, Stn 2-2 (60.70316°N, 02.939989°E), depth 161 m, 24 May 2000; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Oseberg East, Stn 6-1 (60.69365°N, 02.92649°E), depth 159 m, 24 May 2000; collected by A. Sikorski. 1♀ from T. stroemi-complex, Glitne, Stn 2-5 (58.71169°N, 01.667961°E), depth ≈105 m, 30 May 2000; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Balder, Stn 46-5 (59.19403°N, 02.351991°E), depth 123 m, 01 June 2000; collected by A. Sikorski. 1 $\bigcirc$  from *T. stroemi*-complex, Jotun, Stn 13-1 (59.4489°N, 2.362146°E), depth  $\approx$ 115 m, 05 June 2000; collected by A. Sikorski. 1 $\bigcirc$  from T. stroemi-complex, Troll B, Stn 50-4 (60.7272°N, 03.157842°E), depth 321 m, 26 May 2001; collected by A. Sikorski. 299 from 2 specimens of *T. stroemi*-complex, TOGI, Stn 9-3 and 4 (60.5739°N, 03.6194°E), depth 301 m, 28 May 2001; collected by A. Sikorski. 19 from T. stroemi-complex, R/V "Jan Mayen", Duvefjorden, Stn 1121-4 (80.2285°N, 23.21783°E), depth 112 m, 19 September 2001; collected by A. Sikorski. 1♀ from *T. stroemi*complex, Alfa Nord, Stn A5, 1-3 (58° 29.799'N, 01° 43.422'E), depth 108 m, 4–11 September 2003; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Alfa Nord, Stn A5, 0-4 (58° 29.799'N, 01° 43.611'E), depth 108 m, 4–11 September 2003; collected by A. Sikorski. 2  $\bigcirc$  from 2 specimens of *T. stroemi*-complex, Alfa Nord, Stn A1, 0-3 (58° 29.946'N, 01° 43.422'E), depth 108 m, 4–11 September 2003; collected by A. Sikorski. 1♀ from *T. stroemi*complex, Alfa Nord, Stn A11, 1 (58° 29.835'N, 01° 43.118'E), depth 108 m, 4–11 September 2003; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Alfa Nord, Stn Ref, (58° 29.300'N, 01° 43.361'E), depth 108 m, 4–11 September 2003; collected by A. Sikorski.  $9 \bigcirc \bigcirc$  from 3 specimens of *T. stroemi*-complex, Alfa Nord, Stn A8, 0-4 (approx. 58° 29'N, 091° 53'E), depth 108 m, 4–11 September 2003; collected by A. Sikorski. 4

specimens of T. stroemi-complex, SVAN, Stn 1bio-1, 8bio-2 & 3 (approx. 58° 29'N, 091° 53'E), depth 108 m, 4-11 September 2003; collected by A. Sikorski. 1<sup>o</sup>/<sub>+</sub> from T. stroemi-complex, Finnmark, Stn 592-C (70.065°N, 29.0663°E), depth 88 m, 13 September 2003; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  from 2 specimens of T. stroemicomplex, SVAN, Stn ALF 2 (58.50145°N, 01.7242°E), depth 108 m, 20 April 2004; collected by A. Sikorski. 2from 2 specimens of T. stroemi-complex, SVAN, Stn ALF 1-3 (58.49923°N, 01.723466°E), depth 108 m, 20 April 2004; collected by A. Sikorski.  $3 \bigcirc \bigcirc$  from 3 specimens of *T. stroemi*-complex, SVAN, Stn ALF 17 (58.4986°N, 01.7242°E), depth 108 m, 20 April 2004; collected by A. Sikorski. 2♀♀ from *T. stroemi*-complex, Oseberg Øst, Stn 7-3 (60.6873°N, 02.960°E), depth 155 m, 21 May 2004; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Oseberg Øst, Stn 16-2 (60.6746°N, 02.986°E), depth 157 m, 24 May 2004; collected by A. Sikorski. 1 from T. stroemi-complex, Oseberg Øst, Stn 3-1 (60.7069°N, 02.9459°E), depth 158 m, 24 May 2004; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Brage, Stn 10-2 (60.531°N, 03.06337°E), depth 133 m, 27 May 2004; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, TOGI, Stn 10-5 (60.5743°N, 03.654°E), depth 300 m, 01 June 2004; collected by A. Sikorski. 1<sup>o</sup> from *T. stroemi*-complex, TOGI, Stn 11R-4 (60.5727°N, 03.8383°E), depth 298 m, 01 June 2004; collected by A. Sikorski. 1 $\bigcirc$  from T. stroemi-complex, Troll B, Stn 8-5 (60.7508°N, 03.4456°E), depth 325 m, 02 June 2004; collected by A. Sikorski. 1♀ from T. stroemi-complex, Troll C, Stn 1-2 (60.8942°N, 03.582°E), depth 347 m, 03 June 2004; collected by A. Sikorski. 1 $\bigcirc$  from *T. stroemi*-complex, Troll C, Stn 8-5 (60.8942°N, 03.6765°E), depth 340 m, 03 June 2004; collected by A. Sikorski.  $3 \bigcirc \bigcirc$  from T. stroemicomplex, Troll C, Stn 99r-G (61.02043°N, 03.4643°E), depth 350 m, 04 June 2004; collected by A. Sikorski. 1♀ from T. stroemi-complex, Stj Sund, Stn 12-1 (70.279°N, 23.40095°E), depth 401 m, 17 September 2004; collected by A. Sikorski. 1♀ from T. stroemi-complex, Barents Sea, Hopen Bank, Stn 12-2 (75° 55.1'N, 25° 19.2'E), depth 111 m, 24 May 2005; collected by A. Sikorski. 1♀ from T. stroemi-complex, Visund Nord, Stn 5-1 (61.4295°N, 02.557536°E), depth 380 m, 06 June 2005; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  from *T. stroemi*-complex, Vigdis F, Stn 2-5 (61.32626°N, 02.078652°E), depth 235 m, 13 June 2005; collected by A. Sikorski. 1♀ from T. stroemicomplex, Narvik, Stn 10-2 (68.43667°N, 17.34583°E), depth 159 m, 04 July 2005; collected by A. Sikorski. 1♀ from T. stroemi-complex, Resi Stagnes, Stn 7-3 (68° 45.498'N, 16° 35.701'E), depth 93 m, 28 June 2006; collected by A. Sikorski. 1♀ from T. stroemi-complex, Vega, Stn 3-2 (65.69202°N, 12.131583°E), depth 130 m, 04 December 2006; collected by A. Sikorski. 1<sup>o</sup>/<sub>+</sub> from *T. stroemi*-complex, FFH 3958, Stn B3 (65.9283°N, 12.25177°E), depth 105 m, 23 March 2007; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, Nessar, Hopen Bank Stn 20-5 (76° 22.65'N, 27° 38.19'E), depth 109 m, 2007; collected by A. Sikorski.  $3 \bigcirc \bigcirc$  from 3 specimens of T. stroemi-complex, 4475 Eidsfjord, Stn DYP1-1 (68.6987°N, 15.03037°E), depth 159 m, 07 October 2008; collected by A. Sikorski. 4  $\bigcirc$  from 4 specimens of *T. stroemi*-complex, 4475 Eidsfjord, Stn DYP2-1 (68.7092°N, 15.05468°E), depth 147 m, 07 October 2008; collected by A. Sikorski. 1♀ from T. stroemi-complex, 4391 Vannområder Rana, Stn 86S (66.21793°N, 13.59785°E), depth 86 m, 15 October 2008; collected by A. Sikorski. 2  $\bigcirc$  from 2 specimens of *T. stroemi*-complex, Narvik Kom, Stn T2, 2-4 (68.45588°N, 17.43487°E), depth 334 m, 19 July 2009; collected by A. Sikorski.  $2 \bigcirc \bigcirc$  from 2 specimens of *T. stroemi*-complex, 3566 Nessar, Stn G-12-5 (75° 55.23'N, 25° 19.42'E), depth 109 m, 01 October 2009; collected by A. Sikorski,  $5 \oplus 2$  from 5 specimens of T. stroemi-complex, Tysfjord, Stn T3 (67° 53.776'N, 16° 13.393'E), depth 166 m, 14 October 2009; collected by A. Sikorski. 599 from 4 specimens of *T. stroemi*-complex, Mørsvikbotn 2010, Stn Mø 3-1 (67.69995°N, 15.82092°E), depth 157 m, 16 June 2010; collected by A. Sikorski.  $2^{\bigcirc}_{+}$  from 2 specimens of *T. stroemi*-complex, Digermulen, Stn S3-A (66.67955°N, 12.34188°E), depth 210 m, 25 November 2010; collected by A. Sikorski. 1from T. stroemi-complex, Nord Fugløya, Stn S2-A (67.08334°N, 13.86458°E), depth 100 m, 31 March 2011; collected by A. Sikorski. 19 from T. stroemi-complex, Mareano 2012106, Stn 844, sample 101, depth unknown, 10 May 2012; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, 5796 Garn Vest, Stn GAW 02-2 (64.34634°N, 07.728725°E), depth 263 m, 12 June 2012; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, 6489 Suncor, Stn S2 MFB (61.64353°N, 02.09707°E), depth 375 m, 24 July 2013; collected by A. Sikorski. 1♀ from *T. stroemi*complex, 6987 Linesvika, Stn 3A (66.54667°N, 13.32928°E), depth 319 m, 24 March 2014; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, 7178 Kornstad C, Stn 5-3 (62.95308°N, 07.459533°E), depth 181 m, 16 June 2014; collected by A. Sikorski. 1<sup>o</sup> from *T. stroemi*-complex, 7288 Lerøy Vest 2014, Stn Ap3 (60.00465°N, 05.3126°E), depth 350 m, 16 June 2014; collected by A. Sikorski. 1♀ from *T. stroemi*-complex, 7299 Ånholmen, Stn Ånh 2-1 (64.72338°N, 11.44812°E), depth 256 m, 13 August 2014; collected by A. Sikorski. 2stroemi-complex, 7884 Salasbruket 2015, Stn SAL 3-1 (64.79697°N, 11.83655°E), depth 51 m, 24 August 2015; collected by A. Sikorski. 1<sup>♀</sup> from *T. stroemi*-complex, 7886 Daljorda, Stn Da 3-2 (68.68988°N, 14.96113°E), depth

181 m, 24 September 2015; collected by A. Sikorski. 1 $\bigcirc$  from *T. stroemi*-complex, 8190 Hammer ASC, Stn C2-2 (67.96502°N, 15.1663°E), depth 108 m, 31 March 2016; collected by A. Sikorski. NHMUK Reg. Nos 2016.563-572. 1 mature  $\bigcirc$  with 3  $\bigcirc$  on gill stalk of *T.shetlandica*, (APEM), site KVE1-2 Solund (61° 00.025'N, 04° 44.803'E), depth 66 m, 13 June 2017. 1 ovigerous  $\bigcirc$  with 3  $\bigcirc$  on dorsum of *T. shetlandica*, (APEM), site JOR2-2 Finnoy (59° 17.907'N, 05° 56.325'E), depth 366 m, 01 June 2017.

**British material examined**:  $5 \[mu] \]$  from 3 specimens of *T. stroemi*-complex, northern North Sea (near Faeroes), UKCS 210/29, Stn 68-9678, depth 160 m, collection date unknown; collected by R. Bamber. 1 ovigerous  $\[mu] \]$  with 2  $\[mu] \]$  detached from host, APEM project, North Sea, location UKCS 13/24 Bagpuss, ENV1-B collection data unknown. 1 ovigerous  $\[mu] \]$  on "host", APEM project 413646, location UKCS 9/13 Beryl, A9-MFA, location UKCS 9/13 Beryl collection data unknown. 1 mature  $\[mu] \]$  on "host", APEM project 413646, location UKCS 9/13 Beryl, A9-MFA, location UKCS 9/13 Beryl, B8-MFA, collection data unknown. 1 ovigerous  $\[mu] \]$  from "host", (APEM), North Sea, location GG1-FA (57° 13.5512'N, 01° 59.6894'E), depth 96 m, 04 August 2018; collected by Fugro EMU Ltd. 1 immature  $\[mu] \]$  from "host", (APEM), North Sea, location GG2-FA (57° 13.0762'N, 01° 58.9468'E), depth 94 m, 04 July 2013; collected by Fugro EMU Ltd. 1 ovigerous  $\[mu] \]$ , 3 immature  $\[mu] \]$  from 2 specimens of *T. shetlandica* CNS 72, collection data unknown. collected by P. R. Garwood. 3 ovigerous  $\[mu] \]$  from 3 specimens of *T. shetlandica*, RMA CORDAH locality data unknown, 11 December 2003; collected by P. R. Garwood. 1 ovigerous  $\[mu] \]$  on *T. shetlandica* (APEM), Stn GBRCUGR\_14, Curlew Field, North Sea (56° 44.205'N, 01° 36.690'E), depth 98 m, 23 July 2016; collected by Fugro EMU Ltd. 1 ovigerous  $\[mu] \]$  on *T. shetlandica*, (APEM), Stn GBRCUGR\_24, Curlew Field, North Sea (56° 43.164'N, 01° 41.426'E), depth 93 m, 22 July 2016; collected by Fugro EMU Ltd. NHMUK Reg. Nos 2018.163-172.

**Differential diagnosis.** Female ectosoma dorso-ventrally flattened, tapering towards anterior end from maximum width located near posterior end (Fig. 15E, F), ectosoma about 2.07 times longer than maximum width (range 1.6 to 2.69 times longer); mean ectosoma length 1.41 mm, with range of 0.88 to 2.07 mm (based on 10 ovigerous specimens), mean greatest width 0.69 mm (range 0.44 to 1.12 mm), mean depth 0.55 mm (range 0.31 to 0.92 mm). Genital apertures carried on small swellings on posterior margin, separated by distinct gap greater than width of each swelling. Paired cement glands curved, extending only over about posterior 25% of ectosoma length Fig. 15E, F). Egg sacs multiseriate (Fig. 15G); varying from slightly curved to loose spiral in form; typically about 1.1 times longer than ectosoma, varying from shorter than to 1.5 times longer than ectosoma; mean length 1.62 mm (range 0.86 to 2.90 mm).

**Remarks**. Levinsen (1878) based his description of *M. terebellidis* on a single adult female from Greenland, and this species was commonly confused with *M. steenstrupi* prior to the careful documentation of the differences between them by Bresciani & Lützen (1961) which led to the establishment of the latter. Bresciani & Lützen (1961) considered that the most reliable characters for identifying the adult female of *M. terebellidis* are its relatively large body size, up to 4.0 mm, and the limited extent of the cement glands which extend over only about the posterior quarter of the ectosoma, as figured by Levinsen (1878). After examination of large samples of both *M. terebellidis* and *M. steenstrupi*, we found that ectosoma shape is the most useful character. All the *M. terebellidis* found on their hosts by O'Reilly (2016) were attached to the anterior dorsum whereas the *M. steenstrupi* were attached to the gill or the gill stalk. One of the Norwegian specimens of *M. terebellidis* found here (penultimate specimen cited above) was found on the gill stalk of its host. This seems to be an unusual location for this parasite, although Levinsen (1978) in the type description did highlight a juvenile female attached to the host gill.

The body size cited by Bresciani & Lützen (1961) for *M. terebellidis* was up to 4.00 mm, whereas the largest specimen in our collection that exhibited this tapering, flattened ectosoma shape was 2.07 mm. O'Reilly (2016) reported an average length of 1.1 mm (range 0.61 to 1.60 mm) for a large sample of ovigerous females of *M. terebellidis* taken mostly from the northern North Sea, but including some from the southern North Sea, Celtic Sea and from Kosterfjord (Sweden). The largest specimen he recorded from Scottish waters was 1.6 mm in length and carried egg sacs 2.2 mm long. The mean and range of ectosoma sizes exhibited by the ovigerous females in our materal is very similar to that reported by O'Reilly, although the maximum size (2.07 mm long and with egg sacs 2.9 mm) was longer. The size variation is very marked and it is possible that this is indicative of cryptic taxonomic diversity.

The polychaete *Terebellides stroemi* was originally recorded as the host of both *M. terebellidis* and *M. steenstrupi*, but *T. stroemi* has recently been shown to be a species complex (Parapar *et al.* 2011, 2016). O'Reilly (2016) reported *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2015 as host of *M. terebellidis* in British and

Swedish waters. Above we reported the discovery of *M. streenstrupi* on *T. atlantis*, as well as on *T. stroemi*complex. A recent investigation of the genetics of *Terebellides* in the North East Atlantic (Nygren *et al.* 2018) indicated that more than 25 species occur in the area, of which only seven have been formally described. Future studies may reveal comparable diversity within the parasitic copepods that exploit these polychaetes, but molecular evidence will undoubtedly be needed to support the very limited morphological evidence available from these highly modified and reduced parasites.

The male of *M. terebellidis* was briefly described by O'Reilly (2016) who noted that it was similar to that of *M. steenstrupi* as described by Bresciani & Lützen (1961). The male described by O'Reilly (2016) had a body length of about 140 µm, slightly smaller than the male described here for *M. ergasiloides*.

#### Genus Trichobranchicola gen. nov.

**Diagnosis**. Adult female body highly transformed, ectosoma comprising anterior cephalothorax, broad trunk and posterior genitoabdomen, connected to small bulla-like endosoma via narrow stalk. Cephalothorax comprising ventrally-projecting frontal region bearing paired antennules distally and antennae near midline close to narrow stalk, and broader posterior region joining to trunk and bearing paired maxillae at base of frontal process. Trunk dorsoventrally flattened, unsegmented, with 2 pairs of lateral setae located posteriorly. Cement glands paired, extending through posterior third of trunk. Genitoabdomen much shorter than wide; bearing large, paired genital apertures plus, on posterior margin, small median prominence with anal slit. Antennule cylindrical, located at distal corner of projecting frontal process and armed with single apical seta. Antennae located near midline of frontal process between antennules; 2-segmented, proximal segment unarmed, distal segment with paired adhesion pads. Maxillae carried on swellings at base of frontal process, unsegmented but distally subdivided into lobate apical pads. Paired setae present laterally on trunk, possibly representing legs 4 and 5. Egg sacs uniseriate, with up to 6 eggs.

Adult male ovoid, indistinctly divided into anterior cephalothorax and posterior trunk. Cephalothorax bearing paired antennules frontally plus antennae; maxillae located laterally. Oral region indistinct. Trunk lacking defined limbs. Caudal rami apparently absent. Antennules unsegmented, unarmed. Antennae 2-segmented with paired apical pads. Maxillae with robust proximal segment and tapering distal segment.

Type species: Trichobranchicola antennatus gen. et sp. nov., by original designation.

**Etymology**. The name of the new genus is based on a combination of *Trichobranchus*, the name of the host genus, and *–icola*, meaning inhabitant: gender masculine.

**Remarks**. The new genus can be distinguished from *Melinnacheres* by its body form and the arrangement of its paired appendages. The new genus has a bipartite cephalothorax with a conspicuous ventrally-projecting frontal region which carries paired cylindrical processes, interpreted here as antennules, as well as the typical saccopsine antennae, with paired distal adhesion pads. This frontal region has a narrow base relative to the rest of the cephalothorax which broadens out as it merges into the trunk, but it remains separated from the trunk by a slight surface ridge. The broader posterior part of the cephalothorax carries paired maxillary swellings dorsolaterally. These carry lobate maxillae which are subdivided distally, forming apical pads that appear to assist with attachment to the host. The figured specimen (Fig. 16C) was attached to the host by its stalk which originates in the frontal region, but the trunk had been forcibly rotated, providing a clear view of the frontal region.

The posterior margin of the trunk is marked by conspicuous paired genital swellings carrying the paired genital apertures, plus a median anal prominence. This morphology is similar to that exhibited by some *Melinnacheres* species. Paired cement glands are present in the posterior third of the trunk, with the wider anterior part of each gland forming a swelling visible on the lateral margin of the trunk, and curving posteriorly back towards genital apertures.

The form of the 2-segmented female antennae with paired distal adhesion pads, is the same as in *Melinnacheres* and on the basis of this shared derived similarity, we place the new genus in the Saccopsidae, subfamily Saccopsinae. It can be distinguished from *Melinnacheres* by the form of the bipartite cephalothorax of the adult female with its distinct projecting frontal zone bearing paired lobate, unisetose antennules as well as the paired antennae, and by the dorsolateral location and lobate construction of the maxillae.

#### Trichobranchicola antennatus gen. et sp. nov.

**Type material**: Holotype  $\mathcal{Q}$  from *Trichobranchus sikorskii* Leontovich & Jirkov, in Jirkov, 2001, Askeladd Beta, Stn 9-1 (71.47776°N, 20.44262°E), depth 274 m, 27 June 2007; collected by A. Sikorski; NHMUK Reg. No. 2016.573. Paratype ♀ from *T. sikorskii*, Askeladd Beta, Stn 9-1 (71.47776°N, 20.44262°E), depth 274 m, 27 June 2007; collected by A. Sikorski. Paratype  $\mathcal{Q}$  from *T. sikorskii*, Snorre B, Stn 6-3 (61.52512°N, 02.228659°E), depth 349 m, 07 June 1999; collected by A. Sikorski. Paratype spent ♀ from T. sikorskii, Snøhvit N, Stn SN9-3 (71.49229°N, 21.07569°E), depth 323 m, 19 June 2007; collected by A. Sikorski. Paratype non-ovigerous  $\Im$  from T. sikorskii, Snøhvit SN, Stn 11-2 (71.48632°N, 21.08778°E), depth 326 m, 22 May 2010; collected by A. Sikorski. 2 paratype non-ovigerous QQ from *T. sikorskii*, Regionale IX, Stn 3 (71.74983°N, 20.00045°E), depth 267 m, 31 May 2010; collected by A. Sikorski. Paratype  $\mathcal{Q}$  from *T. sikorskii*, Regionale IX, Stn 6 (71.02718°N, 19.6568°E), depth 194 m, 22 May 2010; collected by A. Sikorski. Paratype  $\bigcirc$  from *T. sikorskii*, Mareano 2010110, Stn 556 (70° 38.38'N, 19° 23.8'E), depth 281 m, 04 August 2010; collected by A. Sikorski. Paratype ovigerous  $\mathcal{Q}$  from T. sikorskii, Marulk, Stn MT1-3 - 4 (65.93923°N, 07.560459°E), depth 370 m, 25 May 2012; collected by A. Sikorski. Paratype ♀ from *T. sikorskii*, Regionale, Stn Reg 18-5 (65.88345°N, 07.850723°E), depth 384 m, 26 May 2012; collected by A. Sikorski. Paratype ♀ from *T. sikorskii*, Linnorm, Stn LN13 (64.48857°N, 06.794608°E), depth 215 m, 07 June 2012; collected by A. Sikorski. Paratype non-ovigerous ♀ from *T. sikorskii*, Draugen, Stn DG3-03-4 (64.33839°N, 07.750162°E), depth 275 m, 11 June 2012; collected by A. Sikorski. Paratype spent  $\bigcirc$  from T. sikorskii, Garn Vest, Stn GAW02-5 (64.34654°N, 07.728725°E), depth 263 m, 12 June 2012; collected by A. Sikorski. Paratype  $\mathcal{Q}\mathcal{Q}$  NHMUK Reg. Nos 2016.574-587.

Additional material:  $1^{\circ}$  from *Trichobranchus glacialis* Malmgren, 1866, Vigdis, Stn 4-3 (61.39162°N, 2.079201°E), depth 279 m, 31 May 1999; collected by A. Sikorski. 1 ovigerous  $^{\circ}$  from *Trichobranchus* sp., Fish, Stn 9-3 (71.77159°N, 21.21137°E), depth 317 m, 23 May 2010; collected by A. Sikorski; NHMUK Reg. No. 2017.166.

Differential diagnosis. Adult female ectosoma highly transformed, comprising anterior cephalothorax, broad trunk and well-defined posterior genitoabdomen (Fig. 16A-C), connected via narrow stalk to bulla-like endosoma. Cephalothorax comprising projecting frontal region bearing paired antennules distally and antennae near midline (Fig. 16E), and broader posterior region joining to trunk and bearing paired maxillae at base of frontal process (Fig. 16C). Frontal region directed ventrally, specimen figured in Fig. 16C with frontal process displaced into anteriorlydirected position. Mean body length 240 µm (range 203–255 µm, measured in dorsal view, i.e. excluding ventrallydirected frontal region); mean greatest width 189 µm, with a range of 151 to 210 µm (based on 9 specimens). Trunk dorsoventrally flattened, unsegmented, with 2 pairs of lateral setae posteriorly (arrowed in Fig. 16C), possibly representing vestiges of legs 4 and 5. Cement glands paired, extending through posterior third of trunk (Fig. 16B, C). Genitoabdomen much shorter than wide; bearing large, paired genital apertures plus, on posterior margin, small anal prominence with median anal slit located dorsally (Fig. 16A). Antennule cylindrical, located at distal corner of projecting frontal process and armed with single apical seta (Fig. 16D). Antennae located near midline of frontal process between antennules (Fig. 16E); 2-segmented, proximal segment unarmed, distal segment with paired adhesion pads. Stalk narrow, positioned in mid-line close to antennae (arrowed in Fig. 16E). Form of bulla-like endosoma unclear. Maxillae carried on swellings (Fig. 16C) at base of frontal process, unsegmented but distally subdivided into lobate apical pads (Fig. 16F). Egg sacs uniseriate, typically with 2 or 3 eggs per sac; mean egg diameter 85 um.

Adult male ovoid, indistinctly divided into anterior cephalothorax and posterior trunk. Cephalothorax bearing paired antennules frontally plus antennae; maxillae located laterally. Oral region indistinct. Trunk lacking defined limbs. Caudal rami apparently absent. Antennules lobate, unsegmented, unarmed. Antennae 2-segmented with paired apical adhesion pads. Maxillae with robust proximal segment and tapering distal segment.

Etymology. The specific name refers to the prominent frontal process bearing the paired antennules and antennae.

**Remarks**. Only a single male was found but it was a collapsed exuvium and in poor condition. It carried three paired appendages and the antennae were of characteristic saccopsine form with paired distal adhesion pads. The maxillae appeared more laterally located than in *Melinnacheres* but the oral region was collapsed. No detail could be ascertained of the posterior extremity of the male body. The male was attached adjacent to a genital aperture of



**FIGURE 16**. *Trichobranchicola antennatus* **gen. et sp. nov**. female. A, adult female detached from host, dorsal; B, same, ventral; C, attached female rotated so frontal region and paired maxillae visible; D, frontal region, frontal view *in situ*; E, frontal region showing paired antennules and antennae, with broken base of stalk arrowed; F, maxilla. Scale bars: A–C, 100  $\mu$ m, D, 50  $\mu$ m, E–F, 25  $\mu$ m.

the female but did not contain spermatophores. The two pairs of setae located laterally in the posterior region of the trunk of the female are interpreted here as probable vestiges of legs 4 and 5. The new genus is the only member of the family Saccopsidae to retain vestiges of trunk limbs.

Although its type host is *Trichobranchus sikorskii*, this parasite also occurs on *T. glacialis* and an unidentified *Trichobranchus* sp. The length of the female from *Trichobranchus* sp. was 242  $\mu$ m, which is the same as that of the material from the type host *T. sikorskii*, but its greatest width was 235  $\mu$ m, which falls outside the range given for the type material. This female carried paired egg sacs, one was damaged and incomplete, but the other contained 6 eggs (mean diameter 114  $\mu$ m), which were larger than those from females on *T. sikorskii*. The single female collected from *T. glacialis* was not ovigerous and was subsequently damaged during dissection from the host. The significance of this variation in body proportions and egg size is not yet apparent, and more material is needed. Currently the known distribution of *T. antennatus* gen. et sp. nov. is limited to waters of western and northern

#### Genus Lanassicola gen. nov.

Norway. The known depth range of this parasite is 194 to 374 m.

**Diagnosis**. Ectosoma of adult female comprising cephalothorax, unsegmented trunk and genitoabdomen; body typically elongate and dorsoventrally flattened; cephalothorax undifferentiated or weakly delineated from post-cephalic trunk by dorsal surface suture. Cephalothorax with or without dorsal and antero-lateral lobes. Ectosoma attached to host via stalk originating anteriorly in oral region and connecting to small discoid endosoma within host. Trunk dorsoventrally flattened, typically about 3 to 4 times longer than wide, lacking vestiges of limbs. Cement glands paired, slender, extending through posterior third of trunk. Paired genital apertures located posterolaterally, not on conspicuous swellings. Posterior margin bilobate, with anus in midline. Egg sacs multiseriate. Antennule lobate. Antenna 2-segmented; distal segment with paired apical adhesion pads. Maxillae comprising basal segment, distal segment with paired apical pads.

Body of adult male ovoid, comprising fused cephalothorax and trunk. Antennules unsegmented, elongate, bearing up to 5 setal elements along anterior and distal margins. Antennae and maxillae as in female. Oral region enclosed by subrectangular chitinous framework, referred to here as oral funnel, containing paired rounded lobes densely ornamented with long setules plus smaller anterior lobe.

Type species: Lanassicola arcticus gen. et sp. nov., by original designation

**Etymology**. The name of the new genus is based on a combination of *Lanassa*, the name of the host genus, and *–icola*, meaning inhabitant: gender masculine.

**Remarks.** The new genus shares with other saccopsids, the typical construction of both the antenna and maxilla. The antenna is 2-segmented and the distal segment carries paired pads apically. The maxillae are located posterior to the stalk and carry 2 adhesion pads apically. This derived limb morphology is shared with *Melinnacheres* and supports the placement of the new genus in the Saccopsinae. The new genus can be distinguished from *Melinnacheres* and *Trichobranchicola* gen. nov. by its elongate and strongly dorsoventrally flattened female body, and by the presence of paired antennules represented by unarmed anterior lobes. The paired genital apertures are less prominent in the new genus than in *Melinnacheres* and *Trichobranchicola* gen. nov.

The body of the male of the new genus is sac-like and shares the possession of paired antennules, antennae and maxillae with the males of both *Melinnacheres* and *Trichobranchicola* gen. nov. The antennules are unsegmented and carry 4 or 5 setal elements. The post-cephalic trunk of male *Melinnacheres* tapers posteriorly and appears to carry paired posterolateral genital openings. No genital apertures are present on the trunk of *Lanassicola* gen. nov. males (see below for discussion of reproductive biology in the Saccopsidae).

The type species, *Lanassicola arcticus* gen. et sp. nov., and the two other new species of *Lanassicola* gen. nov. described below occur on hosts belonging to the subfamily Terebellinae, within the Terebellidae.

#### Lanassicola arcticus gen. et sp. nov.

**Type material**: Holotype ovigerous  $\bigcirc$  from *Lanassa venusta* (Malm, 1874), Stjernsund, Stn 12-1 (70.27983°N, 22.4015°E), depth 402 m, 15 August 2012; collected by A. Sikorski; NHMUK Reg. No. 2015.465. 3 paratype  $\Im \Im$  attached to holotype female; same locality and habitat data.



**FIGURE 17**. *Lanassicola arcticus* **gen. et sp. nov**. female. A, ovigerous female with 3 males attached, ventral view; B, head region, ventral view showing location of antennae (ant) and maxillae (mx) relative to stalk; C, posterior margin of trunk, showing attachment of egg sacs at genital apertures; D, maxilla. Scale bars: A, 0.5 mm, B, 50 µm, C, 100 µm, D, 25 µm.

**Differential diagnosis.** Female body (Fig. 17A) with elongate ectosoma, about 5.8 times longer than wide, connected via short stalk to small bulla within host. Ectosoma dorsoventrally flattened, about 2.19 mm in length and with maximum width of 0.38 mm in anterior half. Frontal margin produced into paired, slightly asymmetrical lobes, probably representing antennules (Fig. 17B). Lateral margins weakly sinuous, widest in anterior half,

narrowing slightly in mid-region, becoming wider posteriorly. Posterior margin terminating in paired posterolateral lobes bearing genital apertures (Fig. 17C). Stalk located on mid-ventral surface close to frontal margin (Fig. 17B), connecting to bulla (endosoma). Bulla small, expanding within host, incomplete. Paired antennae located close to ventral line just anterior to origin of stalk (Fig. 17B, ant). Each antenna 2-segmented; first segment unarmed, second segment bearing paired distal adhesion pads. Maxillae located posterior to stalk (Fig. 17B, mx); each maxilla 2-segmented, with robust first segment and broad second segment bearing 2 distal pads, one strongly corrugated, one smooth (Fig. 17D). Cement glands slender, curved, about 0.4 mm in length, located in posterior quarter of ectosoma.

Male sac-like (Fig. 18A), comprising anteriorly-directed oral funnel plus lobate trunk about 126 µm in length; trunk pear-shaped with narrow anterior end, broadening posteriorly, maximum width of about 77 µm at about two thirds of distance along trunk. Paired antennules located anterodorsally; unsegmented (Fig. 18B), tapering, armed with 4 setae along anterior margin and on apex. Paired antennae located on frontal margin either side of midline (Fig. 18B). Oral region modified into funnel-like structure located anteriorly. Oral funnel enclosing paired spinulate pads. Maxillae similar in structure to those of female, located posterior to oral funnel on ventral surface (Fig. 18A). Male discharging twisted, conical spermatophores from oral funnel; each spermatophore with globular basal part (arrowed in Fig. 18B) attached to surface of female, and tapering distal tubule.



**FIGURE 18**. *Lanassicola arcticus* **gen. et sp. nov**. male. A, habitus, ventral view showing paired maxillae immediately posterior to oral funnel; B, oral funnel, dorsal view showing paired antennules and antennae located just anterior to base of oral funnel, and spermatophore (arrowed) in process of being extruded through oral funnel. Scale bars: A, 50 µm, B, 25 µm.

Etymology. The name of the new species, arcticus, alludes to the type locality within the Arctic Circle.

**Remarks.** The male in figure 18B is in the process of discharging a tapering conical spermatophore. This spermatophore is being extruded via a funnel-like structure in the oral region of the male, and the circular base that adheres to the female emerges first. The spermatophore is attached in the genital region of the female. The spinulate pads in the oral region of the male form part of the extrusion mechanism in *Lanassicola* gen. nov., and we

infer this mechanism is also exhibited by *Melinnacheres* which has the same oral morphology in the male (Fig. 14F) and the same shape of spermatophore (Fig. 14A). This mode of spermatophore transfer, where spermatophores are extruded anteriorly through an opening in the cephalothorax of the male is similar to that described for the members of the family Herpyllobiidae, although the bottle-shaped male herpyllobiids are considerably more reduced and lack specialised structures such as the spinulate pads present in these saccopsine males.

The adult female is positioned in a longitudinal indentation in the host's body, near its anterior end, lying between the worm and its tube, with its head end directed down the tube towards the posterior end of the host.

#### Lanassicola bilobatus gen. et sp. nov.

**Type material**: Holotype ovigerous  $\bigcirc$  from tube of *Lanassa nordenskjoeldi* Malmgren, 1866, Argus Miljø, Stn 2-2 (67° 08.515'N, 15° 24.902'E), depth 245 m, 12 May 2011; collected by A. Sikorski; NHMUK Reg. No. 2015.466. 2 allotype  $\bigcirc \bigcirc \bigcirc$  attached to Holotype female; same locality and habitat data.

**Differential diagnosis**. Adult female ectosoma (Fig. 19A) elongate, about 3.5 times longer than maximum width, connected to small bulla inserted within host, via short stalk. Ectosoma dorsoventrally flattened, about 2.79 mm in length and with a maximum width of about 0.8 mm anteriorly, tapering to a width of about 0.5 mm posteriorly. Cephalothorax with paired frontal and anterolateral lobes. Frontal lobes directed slightly anterolaterally, unarmed, probably representing antennules. Anterolateral lobes expanded dorsally (Fig. 19B). Posterior margin of ectosoma (Fig. 19C) expanded to form median lobe bearing anal slit. Paired genital apertures located ventrally at posterolateral extremities of ectosoma. Cement glands irregularly curved (Fig. 19C), up to 0.6 mm in length. Egg sacs multiseriate, about 3.76 mm in length (Fig. 19A).

Paired antennae located anterior to stalk originating in oral region (Fig. 19B); directed medially. Antenna 2segmented (Fig. 19D); proximal segment unarmed, distal segment with paired corrugated adhesion pads. Maxilla (Fig. 19E) located posterolateral to stalk; comprising robust proximal segment; distal segment with paired corrugated pads.

Male sac-like (Fig. 20A), pear-shaped with narrow anterior end and broad posterior extremity, 110 µm in length, with maximum width of 82 µm. Paired antennules located anteriorly on lateral margin, paired antennae located on frontal margin either side of mid-line (Fig. 20A). Antennules unsegmented (Fig. 20B), tapering, armed with 5 setae along anterior margin and apex. Oral region modified into funnel-like structure located anteriorly on ventral surface. Oral funnel ovoid in ventral view (Fig. 20C), enclosing paired spinulate pads. Maxillae similar in structure to those of female, located posterior to oral funnel on ventral surface (Fig. 20C). Male producing paired cylindrical spermatophores (Fig. 20D) about 30 µm long, each with short tubule.

**Etymology**. The name of the new species, *bilobatus*, alludes to the presence of two pairs of lobes on the frontal margin of the cephalothorax.

**Remarks**. The adult female of *Lanassicola bilobatus* gen. et sp. nov. can be distinguished from *L. arcticus* gen. et sp. nov. by the bilobate frontal margin of the cephalothorax in the former compared to the unilobate condition of the latter. The paired lobes of *L. bilobatus* gen. et sp. nov. are interpreted as representing antennulary and anterolateral lobes. The body of *L. bilobatus* gen. et sp. nov. is also larger, so the body length of the adult female is 2.79 mm, compared to 2.19 mm in the type species, and the trunk is thicker and more robust. The adult male of *L. bilobatus* gen. et sp. nov. is sub-triangular in dorsal view compared to the rounded sac-like trunk of male *L. arcticus* gen. et sp. nov.

The ectosoma was detached from the host and so there is no information on the form of the endosoma, or on the positioning on the host.

#### Lanassicola dorsilobatus gen. et sp. nov.

**Type Material:** Holotype  $\bigcirc$  from *Proclea graffii* (Langerhans, 1884), 6160 Skjerstadfjorden, Stn H2-4 (67.23486°N, 15.3628°E), depth 245 m, 10 September 2013; collected by A. Sikorski; NHMUK Reg. No. 2015.3001. Paratype  $\bigcirc$  from *P. graffii*, Codfarmers, Mørkvedbukta Stn Dyp2-2 (67° 16.528'N, 14° 33.207'E), depth 56 m, 15 July 2009; collected by A. Sikorski; NHMUK Reg. No. 2015.3002.



**FIGURE 19**. *Lanassicola bilobatus* **gen. et sp. nov**. female. A, ovigerous holotype female, lateral view of flexed female bearing 2 males; B, head region, ventral view showing location of antennae and maxillae relative to stalk; C, posterior region of trunk, ventral view showing males attached in vicinity of paired genital apertures; D, antenna; E, maxilla. Scale bars: A, 1.0 mm, B–C, 200 µm, D–E, 25 µm.



**FIGURE 20**. *Lanassicola bilobatus* **gen. et sp. nov**. male. A, habitus, dorsal view showing frontal location of antennules and antennae; B, antennule; C, oral funnel apparatus and paired maxillae; D. isolated spermatophore detached from female. Scale bars: A, 50 µm, B–D, 25 µm.

Additional material: 1<sup>o</sup> from *Leaena abranchiata* (M. Sars, 1865), Buktodden FFH, Stn S1-A (66.30828°N, 13.43095°E), depth 170 m, 26 March 2003; collected by A. Sikorski; NHMUK Reg. No. 2015.3003.

**Differential diagnosis**. Adult female ectosoma dorsoventrally flattened, about 3.3 times longer than wide; comprising indistinctly separated cephalothorax and elongate postcephalic trunk (Fig. 21A, B); mean body length 1.61 mm, ranging from 1.53 to 1.68 mm. Cephalothorax with paired frontal lobes, paired lateral lobes and median hemispherical dorsal lobe. Frontal lobes directed anterolaterally, unarmed, probably representing antennules. Lateral lobes conspicuously expanded dorsally (Fig. 21A); small paired processes present on ventral surface (Fig. 21B) near base of each lateral lobe. Stalk narrow, connecting to bulla inside host. Posterior margin of ectosoma expanded to form small median lobe bearing anal slit (Fig. 21C). Posterolateral corners rounded, bearing paired genital apertures ventrally. Egg sacs multiseriate.

Paired antennae originating anterior to stalk in oral region (Fig. 21B); antennae directed medially. Antenna 2segmented (Fig. 21D); proximal segment unarmed, distal segment with paired apical adhesion lobes. Maxilla located posterolateral to stalk; comprising robust proximal segment densely ornamented with spinules on posterior surface (Fig. 21E) and distal segment bearing paired apical pads.

Male unknown.

**Etymology**. The name of the new species, *dorsilobatus*, alludes to the gross morphology of the cephalothorax of the female which carries a distinct median hemispherical lobe on the dorsal surface.

**Remarks**. This species can be readily distinguished from its congeners by the gross morphology of the cephalothorax. It has paired antennulary lobes on the frontal margin like both of its congeners and it has paired anterolateral lobes as in *L. bilobatus* gen. et sp. nov., but these are absent in the type species, *L. arcticus* gen. et sp. nov. It differs from *L. bilobatus* gen. et sp. nov. in the possession of a conspicuous dorsal lobe on the

cephalothorax which is lacking in the latter. This is also a much smaller species, ranging from 1.53 to 1.68 mm in body length: its congeners have an adult female body length of 2.79 mm in *L. bilobatus* gen. et sp. nov. and 2.19 mm in *L. arcticus* gen. et sp. nov.

The female lies in a deep longitudinal groove in the host, with its anterior end pointing back towards the host's posterior end, as in the type species. Both hosts, *Proclea graffii*, the type host, and *Leaena abranchiata*, belong to the subfamily Terebellinae. The known depth range of the parasite is 56 to 245 m.



**FIGURE 21**. *Lanassicola dorsilobatus* **gen. et sp. nov**. female. A, habitus, dorsal view; B, head region, ventral view showing location of antennules, antennae and maxillae relative to stalk; C, posterior region of trunk, ventral view showing paired genital apertures; D, antenna; E, maxilla. Scale bars: A, 0.5 mm, B–C, 200 µm, D–E, 25 µm.

#### Subfamily Euchonicolinae subfam. nov.

A new subfamily is established to accommodate *Euchonicola* gen. nov. and *Euchonicoloides* gen. nov. These two new genera are placed in the family Saccopsidae because they share the basic body plan of a large ectosoma and a small endosoma connected by a small stalk. Around the base of the stalk are located vestigial antennules (absent in *Euchonicoloides* gen. nov.) and subchelate antennae, but maxillae are lacking. In contrast, members of the subfamily Saccopsinae are characterised by the distinctive form of the antennae, which are 2-segmented and carry paired distal adhesion pads on the apical segment, and by the possession of 2-segmented maxillae which also carry paired apical adhesion pads.

#### Genus Euchonicola gen. nov.

**Diagnosis**. Adult female body highly transformed, comprising large ectosoma connected via short stalk to small flattened, discoid endosoma located within host. Ectosoma indistinctly segmented, comprising fused cephalothorax and trunk plus small abdomen. Abdomen distinct, unsegmented, bearing median anal slit terminally and paired caudal rami. Cement glands paired, conspicuous in posterior part of trunk of mature females. Egg sacs uniseriate. Endosoma flattened, irregularly discoid, typically elliptical and narrower than width of trunk. Ectosoma with 2 pairs of appendages close to base of stalk. Antennules reduced to unarmed lobes. Antennae 2-segmented, subchelate, comprising robust basal segment and curved apical claw. Other mouthparts and swimming legs all lacking. Male unknown.

Type species: Euchonicola caudatus gen. et sp. nov., by original designation.

**Etymology**. The name of the new genus is based on a combination of *Euchone*, the name of the host genus of the type species, and *–icola* meaning inhabitant: gender masculine.

**Remarks**. The organization of the body of the new genus is similar to that of saccopsids, with the entire body (cephalothorax, trunk, and small abdomen) forming an indistinctly segmented and undifferentiated ectosoma attached via a short stalk originating ventrally in the oral area which connects to a small flattened endosoma that lies within the host. The oral origin of the stalk is indicated by the positioning of the vestigial antennules and subchelate antennae around the base of the stalk. In some specimens the body appears to exhibit traces of serial subdivision along the longitudinal axis of the trunk region, however, the grooves between these apparent segments coincide with, and probably express, the spacing of the large eggs contained within the oviduct.

The new genus differs from *Melinnacheres*, *Trichobranchicola* gen. nov., and *Lanassicola* gen. nov. in the structure of the antennae and the lack of maxillae in the adult female. In all three of these saccopsine genera the antennae carry paired adhesion pads distally, whereas in *Euchonicola* gen. nov. the antennae are subchelate, terminating in a curved claw. The saccopsine genera are also characterized by the possession of well developed maxillae bearing paired adhesion pads distally, whereas in *Euchonicola* gen. nov. the maxillae are lacking.

# Euchonicola caudatus gen. et sp. nov.

**Type material:**  $\bigcirc$  Holotype from *Euchone* sp., Regionale 2004, Stn 06-3 (60.5222°N, 03.727°E), depth 295 m, 01 June 2004; collected by A. Sikorski; NHMUK Reg. No. 2015.445.  $\bigcirc$  paratype from *Euchone* sp., Fish 2010, Stn 5-4 (71.78508°N, 21.16853°E), depth 315 m, 23 May 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.3011.  $\bigcirc$  paratype from *Euchone* sp., Snøhvit, Stn SF9-2 (71.61494°N, 21.04817°E), depth 323 m, 09 June 2003; collected by A. Sikorski; NHMUK Reg. No. 2016.588.  $\bigcirc$  paratype detached from host, *Euchone* sp., northern North Sea, NW Hutton Field, BP x 054, 5000N (61.14501°N, 01.30915°E), depth 146 m, summer 2002; collected by P.R.Garwood; NHMUK Reg. No. 2015.3012.

**Differential diagnosis.** Adult female attached to host via short oral stalk connecting ectosoma with discoid, embedded endosoma (Fig. 22A–C). Total length of cylindrical ectosoma 406 to 443  $\mu$ m, with trunk about 2.4 to 2.5 times longer than wide (365–410  $\mu$ m by 160–165  $\mu$ m, respectively); retaining apparent traces of subdivision along body (Fig. 22A) in some specimens, and with distinct abdomen. Stalk located anteriorly on ectosoma (Fig. 22E), with paired lobate antennules and subchelate antennae positioned close to base of stalk. Antennules (Fig. 22F) lobate, unarmed. Antennae (Fig. 22G) comprising broad basal segment with lobate inner margin, and strongly



**FIGURE 22**. *Euchonicola caudatus* **gen. et sp. nov**. female. A, detached female, lateral view; B, same, ventral view; C, attached female (to setiger 8 of host), lateral view showing extent of endosoma drawn through cleared body wall of host; D, posterior extremity, showing divergent, bilobate caudal rami and anus; E, stalk; F, lobate antennule; G, antenna. Scale bars: A–C, 100 μm, D–G, 25 μm.

recurved, claw-like apical subchela: tip of subchela opposing rounded swelling on myxal margin of basal segment when adducted. Ectosoma bearing paired, unarmed, rounded genital lappets posteriorly, marking genital openings. Paired cement glands visible posteriorly in trunk, extending at least half length of trunk. Abdomen distinct, unsegmented, about 2.2 times longer than wide; bearing laterally-directed caudal rami, and with median anal slit (Fig. 22D). Caudal rami divergent; each ramus bipartite with broad proximal part and narrow distal part bearing vestige of single caudal seta apically (Fig. 22D). Egg sacs unknown.

Etymology. The name of the new species alludes to the bipartite state of the caudal rami of the adult female.

**Remarks**. The adult female of the new species has a cylindrical, unsegmented trunk bearing a distinct abdomen posteriorly. The trunk may show signs of subdivision but this probably reflects the presence of a series of relatively large eggs within the oviducts inside the trunk. The caudal rami are bipartite and strongly divergent in this species. Females of the new species occured on unidentified hosts of the sabellid genus *Euchone* Malmgren, 1866 collected from northern Norway and the northern North Sea. Off the coast of Norway, the parasite occurs in waters from 295 to 323 m in depth.



**FIGURE 23**. *Euchonicola linearis* **gen. et sp. nov**. female. A, damaged female attached to setiger 10 of host; B, detail showing abdomen of same specimen; C, trunk and abdomen of female attached to setiger 12 of host. Scale bars: A–C, 100 µm.

#### Euchonicola linearis gen. et sp. nov.

**Type material**: Holotype  $\bigcirc$  from *Chone* sp., Fish 2010, Stn 2-5 (71.79853°N, 21.16865°E), depth 320 m, 23 May 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.3009. Paratype  $\bigcirc$  from *Chone* sp., FFH 3958, Stn B3A (65.92825°N, 12.25177°E), depth 105 m, 23 March 2007; collected by A. Sikorski; NHMUK Reg. No. 2015.3010.

**Differential diagnosis**. Adult female attached to host via short oral stalk connecting ectosoma with discoid, embedded endosoma (Fig. 23A). Total length of cylindrical ectosoma 465 to 530 µm, with trunk about 2 times longer than wide (390 µm by 190 µm, respectively); retaining apparent traces of subdivision along body in some specimens (Fig. 23C), and with distinct abdomen (Fig. 23B). Stalk located anteriorly on ectosoma, with paired antennules and subchelate antennae positioned close to base of stalk. Antennules lobate, unarmed. Antennae comprising broad basal segment with swollen inner margin, and strongly recurved, claw-like apical subchela: tip of subchela opposing rounded swelling on myxal margin of basal segment when adducted. Ectosoma bearing paired, unarmed, rounded genital lappets posteriorly, marking genital openings (Fig. 23C). Paired cement glands visible posteriorly in trunk (Fig. 23A, C), extending over half length of trunk. Abdomen distinct, unsegmented, about 2 times longer than wide; bearing posteriorly-directed caudal rami and with median anal slit (Fig. 23B). Caudal rami parallel; each ramus with slight proximal swelling and narrower distal part; rami unarmed. Egg sacs unknown.

**Etymology**. The name of the new species refers to the posterior orientation of the caudal rami, which are held parallel with the longitudinal axis of the body.

**Remarks**. This species is very similar to the type species *E. caudatus* gen. et sp. nov. but can be distinguished by its relatively large ectosoma, 465 to 530  $\mu$ m in length, compared to 406 to 443  $\mu$ m in *E. caudatus* gen. et sp. nov. The form of the caudal rami also differs: in *E. linearis* gen. et sp. nov. the rami have a slight proximal swelling and are directed posteriorly whereas in *E. caudatus* gen. et sp. nov. they are markedly bipartite and directed laterally. The validity of these characters as specific level discriminants should be tested as more material becomes available.

This species is only known from females found on unidentified specimens of the sabellid genus *Chone* Krøyer, 1856, collected at depths of 105 to 320 m off the coast of northern Norway.

#### Euchonicola parvus gen. et sp. nov.

**Type material**: Holotype ovigerous  $\bigcirc$  from *Euchone* sp., northern North Sea, NW Hutton Field, BP x 054, 10,000N (61.18358°N, 01.30915°E), depth 148 m, summer 2002; collected by P. R. Garwood; NHMUK Reg. No. 2016.589.

**Differential diagnosis**. Ectosoma of holotype contracted showing apparent segmentation of trunk (Fig. 24A). Ectosoma comprising large cephalothorax, 4-segmented trunk and distinct abdomen. Total length of ectosoma 270  $\mu$ m: cephalothorax about 50  $\mu$ m long (in dorsal midline) with maximum width of 118  $\mu$ m, comprising about 19 % of total body length, viewed dorsally. Cephalothorax attached to host via short stalk (Fig. 24B) connecting to ill-defined discoid endosoma embedded in host (Fig. 24A). Post-cephalic trunk subdivided into 3 trunk somites, genital region bearing paired genital apertures, and tapering abdomen. First post-cephalothoracic trunk somite about 45  $\mu$ m long by 117  $\mu$ m wide, second 36  $\mu$ m long by 119  $\mu$ m wide, third about 66  $\mu$ m long by 120  $\mu$ m wide (measured at anterior margin). Abdomen tapering posteriorly; about 46  $\mu$ m long, bearing posteriorly-directed, cylindrical caudal rami. Antennules lobate. Antenna subchelate, with robust basal segment and curved apical claw. Egg sacs uniseriate, each containing 3 large eggs (Fig. 24A).

Etymology. The name of the new species alludes to the small size of this species compared with its congeners.

**Remarks**. The new species can be distinguished from its two congeners (described above) by its relatively small body size. The ectosoma of the ovigerous holotype female is only 270  $\mu$ m in length compared to 406 to 443  $\mu$ m and 465 to 530  $\mu$ m in *E. caudatus* gen. et sp. nov. and *E. linearis* gen. et sp. nov., respectively. The body segmentation appears to be better defined than in both other species but this appearance may be an artefact of contraction of the trunk after extrusion of the egg sacs, and might not therefore be a reliable diagnostic character. The abdomen tapers more markedly in *E. parvus* gen. et sp. nov. than in either *E. caudatus* gen. et sp. nov. or *E. linearis* gen. et sp. nov., and the caudal rami have no proximal swelling.



**FIGURE 24.** *Euchonicola parvus* **gen. et sp. nov**. Holotype. A, ovigerous holotype female attached to setiger 5 of host; dorsal view with extent of endosoma within host indicated; B, frontal margin of head showing location of lobate antennule and subchelate antenna relative to stalk. Scale bars: A, 100  $\mu$ m, B, 25  $\mu$ m.

This species is known only from the holotype which was attached to the fifth setiger of its host, an unidentified species of the sabellid genus *Euchone*. The type locality of *E. parvus* gen. et sp. nov. in the northern North Sea is only 5 km north of one of the sites from where *E. caudatus* gen. et sp. nov. was collected. It is possible both species occur on the same host. Small *Euchone* specimens can be difficult to identify and it was initially thought that the host of *E. parvus* gen. et sp. nov. and perhaps *E. caudatus* gen. et sp. nov. might be the undescribed *"Euchone x"* referred to by Cochrane (2003). However, other new *Euchone* have also been described from the area (Giangrande *et al.* 2017) so designating the hosts of these copepods would require careful re-assessment.

#### Genus Euchonicoloides gen. nov.

**Diagnosis**. Adult female body highly transformed, comprising ectosoma connected via short stalk to flattened endosoma located within host. Ectosoma comprising fused cephalothorax and trunk incorporating abdomen. Endosoma discoid to lobate, with well defined margins. Ectosoma elongate to squat, with or without traces of trunk segmentation. Genital apertures paired, located at posterolateral angles of trunk, either side of vestigial abdomen. Abdomen incorporated into trunk, lacking caudal rami and anal slit. Cement glands paired, conspicuous in posterior part of trunk in mature females. Egg sacs uniseriate or biseriate. Ectosoma with pair of antennae close to base of stalk. Antennae 2-segmented, subchelate, comprising robust basal segment and curved subchela. Antennules, other mouthparts and swimming legs all lacking. Male unknown.

Type species: Euchonicoloides elongatus gen. et sp. nov., by original designation.

Etymology. The name of the new genus alludes to its close resemblance to Euchonicola gen. nov.

**Remarks**. The organization of the body of the new genus is similar to that of *Euchonicola* gen. nov. The type species of both genera share a subchelate antenna that terminates in a curved claw, and both lack maxillae which are present in the saccopsine genera. The new genus differs from *Euchonicola* gen. nov. in the incorporation of the abdomen into the trunk, in the lack of caudal rami and an anal slit on the vestigial abdomen, and in the absence of any vestiges of antennules.

#### Euchonicoloides elongatus gen. et sp. nov.

**Type Material**: Holotype ovigerous  $\bigcirc$  from *Euchone* sp., Mareano 2010110, Stn 556 (70° 38.38'N, 19° 23.8'E), depth 281 m, 04 August 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.524. Paratype ovigerous  $\bigcirc$  from *Euchone* sp., Mareano 2010110, Stn 613 (70° 46.23'N, 20° 49.88'E), depth 246 m, 19 September 2010; collected by A. Sikorski; NHMUK Reg. No. 2015.444. Paratype ovigerous  $\bigcirc$  from *Euchone* sp., Snorre B 02, Stn 7-1 (61.52516°N, 02.247374°E), depth 355 m, 29 May 2002; collected by S. Gagaev; NHMUK Reg. No. 2015.443.

**Differential diagnosis.** Female body comprising elongate ectosoma connected via short, broad stalk to small discoid endosoma embedded within host (Fig. 25A). Ectosoma unsegmented, more or less cylindrical, about 6.2 to 6.3 times longer than wide: length of ectosoma 458 to 528 µm (based on 3 specimens); maximum width 76 to 84 µm. Paired cement glands slender, about 165 µm in length, extending through posterior third of trunk only. Stalk broad, located anteriorly on ectosoma (Fig. 25A, B). Endosoma discoid, narrower than width of trunk; with well defined edges (Fig. 25D). Antennules absent. Antennae positioned posterolateral to base of stalk; comprising robust basal segment and curved apical claw (Fig. 25B, D). Cement glands paired, extending anteriorly to reach about to middle of ectosoma. Genital apertures paired, located posterolaterally on trunk. Abdomen reduced to rounded lobe fully fused with trunk and located dorsally in middle of posterior margin (Fig. 25C); no anal slit present and caudal rami lacking. Egg sacs uniseriate, with up to 10 spherical eggs (Fig. 25B).

**Etymology**. The name of the new species refers to its elongate ectosoma, which is more than six times longer than wide.

**Remarks**. All three of the available specimens carried a single egg sac and the only intact egg sac contained 10 eggs. The eggs were arranged in a single series but the eggs are more or less spherical, not discoid as in caligiform copepods. This parasite is embedded in the head of its host so its egg sacs extend out with the tentacles of the host. Its elongate, cigar-shaped ectosoma which incorporates the abdomen, serves to distinguish this species from its congener described below.

This species is known only from females found on unidentified specimens of the sabellid genus *Euchone* collected at depths between 246 and 355 m off the coast of western and northern Norway.

# Euchonicoloides halli gen. et sp. nov.

**Type material:** Holotype ovigerous  $\bigcirc$  attached to *Jasmineira caudata* Langerhans, 1880, (Unico. 40916), Gardline, Stn ENV05-FB (approx. 44.75°N, 01.78°W), depth 110 m, Acquitaine Basin, Bay of Biscay, 04 May 2007; NHMUK Reg. No. 2015.2995.



FIGURE 25. *Euchonicoloides elongatus* gen. et sp. nov. female. A, ovigerous female, ventral; B, anterior part of ectosoma, stalk and endosoma, ventral view showing position of subchelate antennae; C, posterior part of ectosoma, ventral view shwoing extent of cement glands; D, stalk and antenna, lateral. *Euchonicoloides halli* gen. et sp. nov. Holotype. E, habitus of ovigerous holotype, dorsal. Scale bars: A, E, 100 µm, B–D, 50 µm.



**FIGURE 26.** *Euchonicoloides halli* **gen. et sp. nov**. Holotype. A, female holotype, ventral showing paired bifurcate limbs (?antennae); B, female holotype, lateral showing embedded endosoma. Scale bars: A–B, 100 µm.

**Differential diagnosis**. Ectosoma of holotype contracted showing apparent segmentation of trunk (Fig. 25E): about 230 µm in length (measured in dorsal view) with maximum width of about 175 µm. Ectosoma comprising large cephalothorax, 4-segmented postcephalic trunk and vestigial abdomen (Fig. 26A, B). Cephalothorax about 103 µm long (in dorsal midline) with maximum width of 175 µm, comprising about 45% of total body length, viewed dorsally. Cephalothorax attached to host via short stalk. First to third trunk somites all short and of similar width in dorsal view (Fig. 25E). Fourth trunk somite defined by suture dorsally but fused to third somite ventrally. Paired genital apertures present either side of vestigial abdomen (Fig. 26A). Abdomen represented by rounded lobe in posterior midline, lacking caudal rami and without anal slit. Egg sacs incomplete in holotype, more than twice as long as ectosoma; egg arrangement irregularly biseriate (Fig. 25E). Antennules absent. Antenna comprising broad basal part with curved digitiform distal part functioning as anteriorly-directed subchela (Fig. 26A). Endosoma lobate (Fig. 26B), smaller than ectosoma.

**Etymology**. The new species is named in honour of David Hall (formerly of Unicomarine Ltd., now at Apem Ltd.), who found this material and, over the years, has collected numerous parasitic copepods and kindly made them available for study.

**Remarks**. The new species is placed in *Euchonicoloides* gen. nov. because it shares with the type species, *E. elongatus* gen. et sp. nov., the derived form of the ectosoma in which the abdomen is fully fused to the trunk, and the lack caudal rami and an anal slit. In addition, no traces of antennules are present, whereas lobate antennules are found in the three new species of *Euchonicola* gen. nov. described above.

*Euchonicoloides halli* gen. et sp. nov. differs from the type species in having a short, squat ectosoma which expresses traces of body segmentation in both dorsal and ventral views. In addition, the form of the egg sacs is different, with a uniseriate arrangement of eggs in the type species but an irregularly biseriate arrangement in *E. halli* gen. et sp. nov. The only paired limbs present in adult females of *Euchonicoloides* gen. nov. are the antennae: in the type species they are subchelate with a clearly defined claw (cf. Fig. 25B) whereas in *E. halli* gen. et sp. nov. they comprise a broad basal part with a curved digitiform distal part (Fig. 26A) with the latter apparently functioning as subchela used to attach to host.

The holotype and only specimen was attached in the mid-body of its host, a tiny (3 mm body length) specimen of the sabellid *Jasmineira caudata* caught in the Bay of Biscay.

Another mesoparasite, *Jasmineiricola mackiei* Boxshall, O'Reilly, Sikorski, & Summerfield, 2015 occurs on the same host species in waters around Norway, Sweden, the United Kingdom and Ireland. It bears only a superficial resemblance to *Euchonicolides* gen. nov. and differs in having a large anvil-shaped endosoma with a clearly defined head region and a trunk region with large lateral lobes. There is only a relatively small ectosoma comprising the tip of the genitoabdomen.

# Family Xenocoelomidae Bresciani & Lützen, 1966

This family currently comprises three species placed in two highly transformed genera: *Xenocoeloma* Caullery & Mesnil, 1915 and *Aphanodomus* C.B. Wilson, 1924. The latter is virtually endoparasitic, maintaining only a single opening through the host's body wall through which paired egg sacs are extruded, while *Xenocoeloma* appears to be attached completely externally to the host. Caullery & Mesnil (1919) considered that the body of *Xenocoeloma* is almost entirely covered by the ectoderm of the host, but subsequent studies by Bocquet *et al.* (1968) concluded that the outer membrane covering the body is the modified integument of the copepod and is not of host origin. Both genera possess a posteriorly-located common genital atrium, within which both egg sacs originate. Both genera also exhibit an unusual reproductive strategy, cryptogonochorism, in which the mature adult male is effectively reduced to a testis which is housed within the receptaculum masculinum of the female (Bresciani & Lützen 1972, 1974). The life cycle consists of a dispersal phase, the nauplius, followed by the infective copepodid larva which penetrates the polychaete host, and a parasitic phase. The developmental stages within the host have been summarised by Bresciani & Lützen (1974, fig. 42).

#### Genus Xenocoeloma Caullery & Mesnil, 1915

**Diagnosis**. Adult female body ovoid to cylindrical, highly transformed and lacking traces of external segmentation. Body up to about 6 mm in length. Anterior end attached to host body wall; anterior axopore connecting central axial cavity (axocoel) of copepod with host body cavity. Limbs lacking. Posterior end of body with integumentlined, common genital atrium containing paired oviduct openings and opening to exterior via single atriopore. Egg sacs paired, elongate, multiseriate. Mature adult male reduced to testicular tissue housed within median receptaculum masculinum of female.

Type species: Xenocoeloma brumpti Caullery & Mesnil, 1915.

**Remarks**. *Xenocoeloma* currently comprises two species: *Xenocoeloma alleni* (Brumpt, 1897), a parasite of *Polycirrus caliendrum* Claparède, 1869 and *P. aurantiacus* Grube, 1860, and *X. brumpti*, a parasite of *P. arenivorus* (Caullery, 1915). Caullery & Mesnil (1919) explored in detail the morphology and internal anatomy of *X. brumpti* and presented comparisons with *X. alleni*. They considered that the strongest argument for separating *X. brumpti* as a distinct species was its utilization of a different host from *X. alleni*. This argument is largely based on an assumption of strict host specificity which was prevalent at the time. These species utilize congeneric hosts and both were originally described from opposite shores of the English Channel, *X. alleni* from Plymouth on the coast of the United Kingdom (Brumpt 1897), and *X. brumpti* from the vicinity of Luc-sur-Mer on the coast of Normandy, France (Caullery & Mesnil 1919).

There are morphological differences between the two species: in *X. brumpti* the length of the adult female is 5 to 6 mm and the width (diameter) is 1.25 mm, giving a length:width (L:W) ratio of about 4.0–4.8:1, whereas *X. alleni* has a length of 4 mm and a width of 2 mm, giving a L:W ratio of about 2:1 (Caullery & Mesnil 1919). Bocquet *et al.* (1965) studied *Xenocoeloma* parasitic on *Polycirrus caliendrum* collected at Roscoff: their specimens measured 2.3 mm in length and 1.2 mm in width (after fixation in Bouin's) and they identified them as *X. alleni* on the basis of this L:W ratio of 1.94:1. Differences in coloration have also been reported between these two species (see Bocquet *et al.* 1965), but the summary of coloration patterns given by Gotto (1993) highlights the variability in both body and egg sac coloration. Bocquet *et al.* (1970) studied the development of the genital system in *X. alleni*.

Our material includes *Xenocoeloma* specimens from six different polychaete hosts taken in Norwegian waters, all members of the family Terebellidae. Five of these hosts, *Amaeana trilobata* (M. Sars, 1863), *Polycirrus norvegicus* Wollebaek, 1912, *P. latidens* Eliason, 1962, *P. medusa* Grube, 1850, and *P. plumosus* (Wollebaek, 1912), are all members of the subfamily Polycirrinae, while the other host is *Paramphitrite birulai* (Ssolowiew, 1899), a member of the subfamily Terebellinae. It is possible that cryptic species occur on different hosts. Among hosts of the genus *Polycirrus* Grube, 1850 the situation is compounded by unresolved taxonomic confusion regarding species found in European waters (Glasby & Hutchings 2014).

# Xenocoeloma alleni (Brumpt, 1897)

#### Syn: Saccopsis alleni Brumpt, 1897

Scandinavian material examined: 1º from Polycirrus medusa Grube, 1850, Huldra, Stn 1-1 (60.85328°N, 02.650849°E), depth 123 m, 4 June 1999; collected by A. Sikorski. 19 from *P. medusa*, Balder 2000, Stn 10-4 (59.17966°N, 02.414501°E), depth unknown, 31 May 2000; collected by A. Sikorski.  $1^{\circ}$  from P. medusa, Prosj 2302, Smeerenburgfjord 4, Stn 04-5 (79.74367°N, 11.11°E), depth 203 m, 14 May 2003; collected by A. Sikorski. 1♀ from *P. medusa*, Hydro 2003, Stn 1-5 (72.55416°N, 20.98141°E), depth 393 m, 13 June 2003; collected by A. Sikorski. 1♀ from *P. medusa*, Hydro 2003, Stn 2-3 (72.53105°N, 21.05106°E), depth 372 m, 14 June 2003; collected by A. Sikorski. 1♀ from *P. medusa*, Veslefrikk, Stn 10-1 (60.7857°N, 02.89033°E), depth 171 m, 23 May 2004; collected by A. Sikorski. 1♀ from *P. medusa*, Oseberg Øst, Stn 18-1 (60.7127°N, 02.9082°E), depth 152 m, 25 May 2004; collected by A. Sikorski. 1♀ from P. medusa, Sandnessjøen 2007, Stn Lå3-B (66.23202°N, 12.35218°E), depth 38 m, 03 January 2007; collected by A. Sikorski.  $2\Im \Im$  from 2 specimens of *P. medusa*, Sandnessjøen 2007, Stn Lå2-B (66.23468°N, 12.33743°E), depth 45 m, 03 January 2007; collected by A. Sikorski. 1♀ juvenile attached laterally on mid-body of *Polycirrus latidens*, Sandnessjøen 2007, Stn Lå3-B (66.23202°N, 12.35218°E), depth 38 m, 03 January 2007; collected by A. Sikorski. 3♀♀ from *Polycirrus norvegicus* Wollebaek, 1912, Statfjord A 2005, Stn 4-3 (61.24075°N, 01.887778°E), depth 146 m, 15 June 2005; collected by A. Sikorski.  $1^{\circ}$  from *P. norvegicus*, Codfarmers, Mørkvedbukta Stn DYP2-1 (67° 16.528'N, 14° 33.207'E), depth 56 m, 15 July 2009; collected by A. Sikorski. 1 non-ovigerous ♀ from *Polycirrus plumosus* (Wolleback, 1912), 8132 Hestholmen C, Stn Hest 3-2 (67.15099°N, 14.03847°E), depth 276 m, 05 February 2016; collected by A. Sikorski. 1 nonovigerous ♀ from *P. plumosus*, 8132 Hestholmen C, Stn Hest 1-2 (67.14753°N, 14.02007°E), depth 143 m, 05 February 2016; collected by A. Sikorski. 1♀ from *Polycirrus* sp., Balder, Stn 16-3 (59.1757°N, 02.3778°E), depth 125 m, 26 May 1997; collected by A. Sikorski. 1♀ from *Polycirrus* sp., Balder, Stn 31-5 (59.1877°N, 2.435°E), depth 125 m, 27 May 1997; collected by A. Sikorski. 1 ovigerous  $\bigcirc$  and 1 developing immature  $\bigcirc$  from Amaeana trilobata (M. Sars, 1863), Vigdis PT2, Stn 11-5 (61.37356°N, 02.115149°E), depth 281 m, 12 June 2005; collected by A. Sikorski; NHMUK Reg. No. 2017.478.

**British material examined**: 1 ovigerous  $\mathcal{Q}$  detached from host (*Polycirrus plumosus*) but ovisac entangled in host tentacles, Dove Marine Lab., Stn M1 (=Stn 26), depth 48 m, collected by P.R.Garwood, 08 March 1994 (see O'Reilly & Geddes, 2000). 1 ovigerous ♀ on *Polycirrus* sp.(medusa?), north Irish Sea, Block 109, Stn 12 (53° 54' 51.3"N, 04° 15' 58.7"W) depth 44 m, collected by Sue Hamilton, September 1995. 2 ♀♀ on single Polycirrus *medusa*, north Irish Sea, Block 112, Stn unknown, collected by Sue Hamilton, September probably 1995. 1  $\bigcirc$  from Polycirrus plumosus, Northumberland, Dove Marine Lab., Stn M1 (= Stn 26), depth 48 m, collected by P.R.Garwood, 04 September 1996 (see O'Reilly & Geddes, 2000). 1 ovigerous ♀ on Polycirrus norvegicus (Unico sample 18383), Liverpool Bay, CEFAS Stn M10 (53° 31'N, 03° 31'W), collected 05 September 1996. 1 ovigerous , 1 mature on *Polycirrus* sp. (Unico sample 21664), Liverpool Bay, ERM Day Grab 49a (53° 32.196'N, 03° 29.995'W), collected 30 July 2001. 1 ovigerous  $\mathcal{Q}$ , detached (with *Polycirrus norvegicus*). (Unico sample 25309), Liverpool Bay, Day Grab M10x 13d (53.4408°N, 03.8207°W), collected August 2001. 1 immature ♀ attached to oral area of P. norvegicus, Unico 37927, English Channel, CEFAS, Stn EC 5, sample 232a, (50.50015°N, 01.99826°W), collected September 2005. 1 immature  $\mathcal{Q}$  attached to abdomen of *Polycirrus* sp?, Unico. 37932, English Channel, CEFAS, Stn EC 29, sample 236c, (50.30227°N, 01.96289°W), collected September 2005. 1 ovigerous  $\bigcirc$  on frontal cushion of *Polycirrus* sp., (Unico 41477), Irish Sea, CEFAS Stn ISB55c (54° 00'N, 04° 00'W), depth unknown. 1 mature  $\bigcirc$  on dorsal cushion of *Polycirrus ?norvegicus*, (Unico 44294), CEFAS, Tyne,

Stn NT6c, collected 2007. 2 mature  $\bigcirc$  on *Polycirrus* sp. (Unico 47765), survey EHS WFD, Down Coast, South Rock, Stn SRK-b (54.41908°N, 05.39333°W) depth 24 m ,collected 09 July 2010 by Tim Mackie. 2 mature  $\bigcirc$  on lip of *P. plumosus*, North Kishorn, Stn. 161mW, collected by Sue Hamilton, April 2012. 1 immature  $\bigcirc$  on *P. plumosus*, NW Hutton Field, BPx054, 7.5km N (61.1643°N, 01.3091°E) depth 145 m, collected by P.R. Garwood, 2015? 1 ovigerous  $\bigcirc$  on *Polycirrus* sp. fragment, North Norfolk, Cromer Shoals MCZ, (APEM) Stn 169, CSC B040 (52° 57.066'N, 01° 29.388'E), depth 19 m, 12 September 2014. 1 mature  $\bigcirc$  on *Polycirrus* sp., Shetland, Bow of Hascosay, SEPA Stn 200mW (60.61181°N, 01.0108560°W.), depth 13 m, collected 02 June 2017. NHMUK Reg. Nos 2018.173-182.

**Descriptions**. Six ovigerous females from *Polycirrus medusa* caught in Scandinavian waters were measured: mean ectosoma length was 1.92 mm (range 0.88 to 2.73 mm), mean maximum width of ectosoma was 0.74 mm (range 0.44 to 1.10 mm); mean L:W ratio 2.31:1 (range 1.79 to 3.10:1). The egg sacs are multiseriate, slightly curved and up to 4.5 mm long for largest adult female (2.73 mm ectosoma length). The ectosoma of an ovigerous female from *P. medusa* in the northern Irish Sea measured 1.27 by 0.69 mm, a L:W ratio of 1.83:1, and two non-ovigerous but mature females from the same host and geographical area had L:W ratios of 2.0:1 and 2.17:1.

The material from *Polycirrus norvegicus* included 2 ovigerous adult females (Fig. 27B) emerging from the head of the host. Each has a cylindrical ectosoma: ectosoma lengths were 1.28 and 1.36 mm, and widths 0.56 and 0.70 mm, respectively, giving L:W ratios of 1.94:1 to 2.29:1. The egg sacs are multiseriate, slightly curved and about 1.1 to 1.2 mm long.

The Scandinavian material from *Polycirrus plumosus* comprised 2 non-ovigerous adult females each emerging from the head of its host. Each has a cylindrical ectosoma: ectosoma lengths were 1.69 and 2.38 mm by 0.73 and 0.77 mm wide, respectively, giving a L:W ratio of 2.32:1 to 3.09:1. Ovigerous females from *P. plumosus* caught in the North Sea off Northumberland measured 2.39 by 0.81 mm, a L:W ratio of 2.95:1, and 4.04 by 1.19 mm, a L:W ratio of 3.39:1.

Ovigerous females from unidentified *Polycirrus* sp. collected in British waters exhibited a length range of 1.04 to 1.96 mm and a width range of 0.42 to 0.96 mm. The range of L:W ratios was 1.80:1 to 2.82:1.

The ovigerous adult female from *Amaeana trilobata* has a stout cylindrical ectosoma (Fig. 27A) about 1.47 mm long by 0.84 mm wide, giving an L:W ratio of about 1.75:1. It is attached at its anterior end and the common genital pore lies in the middle of its posterior surface. Both paired egg sacs originate from the common pore. The egg sacs are multiseriate, slightly curved and about 1.95 mm long; each egg sac becomes slightly wider posteriorly. The immature female from the same host has a cylindrical ectosoma 0.67 mm long by 0.34 mm wide (L:W ratio 1.97:1). It lacks any trace of a posterior genital pore.

**Remarks**. This material is all tentatively attributed to *X. alleni* solely on the basis of the L:W ratio of the ectosoma of ovigerous females. The material from *P. medusa* exhibits ratios varying from 1.79:1 up to 3.10:1, and this range encompasses the variation shown by material from all the other hosts except the ovigerous female from *Amaeana trilobata*, which was 1.75:1. One female from *Polycirrus plumosus* caught in the North Sea, off the coast of Northumberland was recorded by O'Reilly & Geddes (2000) as *X. alleni*. This specimen had the highest value for the L:W ratio, 3.39:1. This value falls outside the range of 1.79 to 3.10:1, which we found was typical for *X. alleni*. None of the specimens attains a L:W ratio approaching the 4.0–4.8:1 given for *X. brumpti*. However, with so few morphological features, all these identifications should be regarded as in need of validation once molecular diagnostics become available.

# Xenocoeloma brumpti Caullery & Mesnil, 1915.

**Material examined**: 4 ovigerous  $\bigcirc \bigcirc$  from *Polycirrus norvegicus*, Liverpool Bay, Unicomarine 18443 Stn M10, (53° 31'N, 03° 31'W), depth unknown, 05 September 1996. NHMUK Reg. Nos 2018.183-186. 2 ovigerous and 2 mature  $\bigcirc \bigcirc$  from *Polycirrus* sp., Liverpool Bay, CEFAS (Unico 29118 CEFLBY), (53.5217°N, 03.52147°W), depth unknown, September 2002.

**Descriptions**. Four ovigerous females from *P. norvegicus* were measured: mean ectosoma length was 2.29 mm (range 1.69 to 2.93 mm), mean maximum width of ectosoma (Fig. 27C) was 0.63 mm (range 0.50 to 0.75 mm); mean L:W ratio 3.66 (range 3.42:1 to 3.90:1). The egg sacs are multiseriate, slightly curved and up to 2.4 mm long for largest adult female (2.93 mm ectosoma length).



**FIGURE 27.** *Xenocoeloma alleni* (Brumpt, 1897). A, ectosoma of ovigerous female from *Amaeana trilobata*; B, ectosoma of ovigerous female from *Polycirrus norvegicus* caught in Norwegian waters. *Xenocoeloma brumpti* Caullery & Mesnil, 1915. C. ectosoma of ovigerous female from *Polycirrus norvegicus caught* in Liverpool Bay. *Xenocoeloma orbicularis* **sp. nov**. ovigerous female holotype. D, ectosoma, dorsal view showing paired eggs sacs emerging from common pore; E, same, lateral. *Aphanodomus terebellae* (Levinsen, 1878) adult female, F, habitus with 1 multiseriate and 1 spent egg sac. Scale bars : A, B, C, F, 1.0 mm; D, E, 0.5 mm.

**Remarks**. The material from *P. norvegicus* is tentatively attributed to *X. brumpti* solely on the basis of the L:W ratio of the ectosoma: the mean ratio was 3.66:1. This is less than 4.0:1, the lower limit of the range given by Caullery & Mesnil (1915, 1919). The range exhibited by specimens here attributed to *X. brumpti* was 3.42 to 3.9:1 and it is effectively contiguous with the range of 1.75:1 up to 3.39:1 found here for *X. alleni*. Now that larger samples from a wider range of hosts have become available for study, we find that there is no clear gap between the two species in the L:W ratio. Our dividing line between *X. alleni* (L:W ratio less than 3.40:1) and *X. brumpti* (more than 3.40:1) is arbitrary. As commented for *X. alleni* above, morphology based identifications such as these should be regarded as in need of validation once molecular diagnostics become available.

#### Xenocoeloma orbicularis sp. nov.

**Type Material**: Holotype ovigerous  $\bigcirc$  attached to head of *Paramphitrite birulai* (Ssolowiew, 1899), Statfjord B, Stn 3-5 (59.1735°N, 01.843177°E), depth 144 m, 20 June 1999; collected by A. Sikorski; NHMUK Reg. No. 2015.3035.

**Differential diagnosis**. Female body orbicular with flattened underside (Fig. 27D, E); maximum length 0.87 mm, maximum width 0.95 mm, maximum height in lateral view 0.80 mm. Body lacking traces of segmentation and without vestiges of paired limbs. Egg sacs paired, both egg sac stalks originating from common genital aperture located posterodorsally on body (Fig. 27E); egg arrangement multiseriate; egg sac length unknown (both sacs incomplete in holotype). Body attached to host via broad, featureless stalk, located on ventral surface just anterior to middle of body. Colour of body white.

Etymology. The name of the new species refers to the shape of the ectosoma of the mature female.

**Remarks**. This unusual parasite is placed in the Xenocoelomidae because it shares the possession of a posteriorly-located common genital atrium, within which both egg sacs originate. It is placed in *Xenocoeloma* because the body is carried external to the host. The body of the ovigerous female differs markedly in proportions from the two previously described species of *Xenocoeloma*: in *X. brumpti* and *X. alleni* the L:W ratio of the cylindrical ectosoma of the adult female is 3.42 to 4.8:1 and about 1.75 to 3.39:1, respectively, whereas in the new species the body is wider than long and is orbicular rather than cylindrical. The establishment of a new species to accommodate this single specimen should be treated as a working hypothesis to be tested when more material and molecular data are available.

The host of the new species belongs to the subfamily Terebellinae and, given that all other known hosts of *Xenocoeloma* species belong to the subfamily Polycirrinae, the utilization of a host from a different subfamily could be interpreted as supporting evidence justifying the establishment of the new species. However, as noted below, another xenocoelomid, *Aphanodomus terebellae*, has now been reported from six different hosts also representing two subfamilies of Terebellidae.

# Genus Aphanodomus C.B. Wilson, 1924

**Diagnosis**. Body of adult female highly transformed, lacking any traces of segmentation. Body transversely elongate with paired egg sacs emerging from integument-lined, common genital aperture located posteriorly, in mid body (Fig. 27F). Maximum dimension (body width) of female ranging from 3 mm to 5 mm. Anteriorly, body with axopore opening into axocoel within parasite and connecting to body cavity of host. Mature adult male reduced to testis housed within receptaculum masculinum in female. Nauplius lecithotrophic, lacking naupliar eye.

Type species: Aphanodomus terebellae (Levinsen, 1878) by original designation.

**Remarks**. The genus *Aphanodomus* was established by Wilson (1924) as a replacement name for *Crypsidomus* Levinsen, 1878, which was preoccupied by *Crypsidomus* Günther, 1864 (Reptilia). The organization of the highly modified body of *Aphanodomus* is similar to that of *Xenocoeloma* (Bresciani & Lützen 1974). The major morphological difference between the adult females is the elongate cylindrical to globular body with pores at each end in *Xenocoeloma*, compared to the irregularly cucumber-shaped body of *Aphanodomus* with pores in middle of the long sides (anterior and posterior). The early stage male of *Aphanodomus* is a simple vesicle lying within the

thin walls of squamous epithelium, and it takes up the shape of the receptaculum masculinum. The later stage male differentiates into a functional testis (Bresciani & Lützen 1974).

# Aphanodomus terebellae (Levinsen, 1878)

#### Syn: Crypsidomus terebellae Levinsen, 1878

Scandinavian material examined: 1 ovigerous  $\bigcirc$  from *Leaena abranchiata*, ECASA, Stn Ref-3 (69.883633°N, 19.43823°E), depth 55 m, 17 July 2006; collected by A. Sikorski; NHMUK Reg. No. 2015.2996. 1 ovigerous  $\bigcirc$  from *Artacama proboscidea* Malmgren, 1866, Loppa, Stn D2-2 (70° 08.690'N, 22° 17.708'E), depth 242 m, 24 June 2006; collected by A. Sikorski; NHMUK Reg. No. 2015.2997.

**British material examined**: 1 ovigerous  $\bigcirc$  from *Polycirrus plumosus*, Loch Creran, Fish Farm B, depth unknown, 20 June 1992; NHMUK Reg. No. 2017.483. 1 ovigerous  $\bigcirc$  from *P. plumosus*, Firth of Forth Stn 60 (56° 06.21'N, 02° 40.14'W), depth 46 m, 22 March 2000; collected by Sue Hamilton. 1 ovigerous  $\bigcirc$  from *P. plumosus*, Loch Laxford, Stn 35 (58.39940°N, 05.08402°W), depth 48 m, 12 July 2001; collected by Sue Hamilton. 1 ovigerous  $\bigcirc$  from *P. plumosus*, Loch Sunart, Stn 14 (55.67300°N, 05.92693°W), depth 64 m, 04 August 2001; collected by Sue Hamilton. 1 ovigerous  $\bigcirc$  from *P. plumosus*, Loch Sunart, Stn 14 (55.67300°N, 05.92693°W), depth 64 m, 04 August 2001; collected by Sue Hamilton. 1 ovigerous  $\bigcirc$  from *Polycirrus* sp., Isles of Scilly, (APEM prolect 413059, Sample 8100), Stn GT35 217, collected 2013.

#### Differential diagnosis. As for genus.

**Remarks**. Levinsen (1878) described the ovigerous female of *A. terebellae* and made preliminary observations on its internal anatomy. Bresciani & Lützen (1972, 1974) studied this species in detail and discovered its cryptogonochoristic reproductive strategy. They also showed that the gross morphology of the female is highly variable and it is therefore difficult to confirm specific identity from morphological features alone.

Aphanodomus terebellae has a wide distribution at high latitudes in the northern Hemisphere, from Canada, Greenland, and Iceland, to the Kara Sea in Arctic Russia. Around the British Isles it has been recorded from the Irish Sea (O'Reilly 1995) and in the North Sea off Northumberland (O'Reilly & Geddes 2000). The prevalence of *A. terebellae* on *Lanassa venusta* in the southern Irish Sea varied between 13 and 55% (O'Reilly 1995). The previously reported hosts are: *Amphitrite cirrata* (Müller, 1771, in 1776), *Artacama proboscidea, Lanassa venusta, Nicolea venustula* (Montagu, 1818), *N. zostericola* Örsted, 1844, *Polycirrus medusa, P. plumosus*, and *Thelepus cincinnatus* (Fabricius, 1780). All known hosts belong to the family Terebellidae including the new host recorded here, *Leaena abranchiata*. Given the large number of reported hosts from two different subfamilies within the Terebellidae, it is possible that more than one species of *Aphanodomus* is present in the North Atlantic, but the relative paucity of morphological characters and the variability in gross morphology demonstrated by Bresciani & Lützen (1974), suggests that species differentiation will best be explored using molecular methods.

#### Discussion

Europe has a rich and diverse fauna of ectoparasitic copepods on polychaete hosts (Kim *et al.* 2013). The diversity of new taxa described here indicates that the fauna of mesoparasitic copepods is similarly rich. Securing attachment to living substrate is a challenge for ectoparasites and the evolution of mesoparasitism is one response. Polychaetes represent a particular challenge as their movement typically involves a high degree of body flexure. Polychaetes are typically capable of peristaltic burrowing which involves alternating contraction of circular and longitudinal muscles in the body wall around a coelomic hydrostatic skeleton (Ruppert *et al.* 2004). Active burrowers exhibit waves of contraction along the body. In addition, many polychaetes exhibit slow or fast crawling using parapodia but parapodial movements are commonly accompanied by progressive undulating waves passing along the body, as in phyllodocids, for example. The large females of all the copepods described here secure their attachment to the host by means of an anchor (the endosoma) embedded in the host. In the Bradophilidae, Herpyllobiidae, and Phyllodicolidae this anchor passes through the host's body wall and into the coelom to form a large endosoma that also functions to absorb nutrients from the host. In some saccopsids the anchor is smaller and embeds in the host's body wall itself, as in *Melinnacheres*, but in the new genera *Euchonicola* **gen. nov**. and *Euchonicoloides* **gen. nov**.

the discoid endosoma appears to penetrate deeper and lie within the host's coelom. In contrast, in the Jasmineiricolidae, Pholoicolidae **fam. nov.**, and one genus of Xenocoelomidae, the parasites are virtually endoparasitic with the body itself effectively functioning as the anchor. These forms typically maintain contact with the external environment via the atriopore (in *Aphanodomus*) or via a much reduced genitoabdominal extremity that protrudes out through the host's body wall as in *Pholoicola* **gen. nov**. and *Jasmineiricola*. We consider that the relatively high prevalence of mesoparasitism in copepods utilizing polychaetes as hosts, compared to those using other host taxa, can be viewed as a response to the challenge of maintaining attachment to such a dynamically mobile, living substrate.

Although the polychaetes of European waters are among the best studied in the world, the discovery of five new genera and 13 new species of mesoparasitic copepods from European polychaetes indicates that their parasites remain relatively poorly known and we anticipate that further new taxa will come to light. Moreover the reduced morphology shown by many mesoparastic copepods makes species designation difficult and this, coupled with their wide host range, leads us to believe that there may be some cryptic biodiversity which would only be revealed following DNA studies.

#### Acknowledgements

Most of the specimens examined here have been collected during macrobenthos surveys performed by Akvaplanniva AS, in Norwegian waters, but a variety of other organizations and commercial companies have provided material, mostly from British and Irish waters. We gratefully acknowledge their generosity in making the material available for taxonomic study. We would like to thank Akvaplan-niva AS, Gardline Ltd., Fugro EMU Ltd., Unicomarine Ltd., APEM Ltd., Andy Mackie (National Museum of Wales), Peter R. Garwood (Identichaet, Newcastle-upon Tyne), Jocelyn Richard (Myriad Taxonomy), David Hall (formerly Unicomarine and now APEM Ltd), Sue Hamilton (Edinburgh), John P Hartley (Hartley Anderson Ltd.), Julian Hunter (Hunter Biological Ltd.), Matt Service (Agri-Food & Biosciences Institute, AFBI, Belfast), Tim Mackie (Environment & Heritage Sevices, EHS, Northern Ireland), Keith Cooper (Centre for Environment Fisheries and Aquaculture Sciences, CEFAS, Lowestoft), Jeni Boyle & Stephen Nowacki (Scottish Environment Protection Agency), and the late Roger Bamber (Artoo Marine Biology Consultants) who found some of the specimens studied here and made them available for further study. Material collected by A. Sikorski was taken during sampling supported by the Norwegian Research Council (Project 280724. Environmental monitoring of Arctic coastal ecosystems: sensitivity to petroleum pollution (Arctic EcoSens)).

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